UNIVERSITY OF CANTERBURY

DOCTORAL THESIS

Modelling the Presence-Absence of Multiple Species

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"The first law of ecology is that everything is related to everything else."

Barry Commoner

Abstract

Predicting which species will be present (or absent) across a geographical region remains one of the key problems in ecology. Numerous studies have suggested several ecological forces that can determine species presence-absence: environmental factors (i.e. abiotic environments), interactions among species (i.e. biotic interactions), dispersal and demographic stochasticity. While various ecological forces have been considered, less attention has been given to the problem of understanding how dispersal processes, in interaction with other ecological factors, shape community assembly in the presence of priority effects (i.e. initial abundances determine the presence-absence of species). In this thesis, we investigate the consequences of different dispersal patterns and stochasticity on the occurrence of priority effects and species coexistence in multi-species competitive systems.

By employing deterministic and stochastic models in one-dimensional space, our study shows the conditions under which priority effects occur and disappear as local dispersal strength changes. Without dispersal, priority effects emerge in the presence of intense biotic interactions, with only one species surviving at any given location (i.e. coexistence is impossible). For moderate dispersal levels, dispersal enhances priority effects and promotes multiple species coexistence. Further increasing dispersal strength leads to the disappearance of priority effects and causes extinction of some species. We also demonstrate contrasting observations of stochasticity on priority effects: while priority effects are more prevalent in the stochastic individual-based models (IBM) than in the deterministic models for large populations, we observe fewer occurrences of priority effects in IBM for small populations.

When non-local dispersal is incorporated into the models, priority effects are more pronounced than in the local dispersal models. We also investigate the effects of different dispersal patterns on species coexistence: although very long-range dispersal leads to species extinctions, intermediate-range dispersal permits more outcomes where multi-species coexistence is possible than short-range dispersal (or purely local dispersal). Finally, we extend our model to consider community dynamics in two-dimensional space. We find that knowledge of species' environmental requirements is also crucial

to improving our ability to predict the occurrence of priority effects across heterogeneous environments.

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Hafiz developed the models and performed numerical simulations, with suggestions and input from Rua Murray, Michael Plank and William Godsoe. All authors interpreted and discussed the results. Hafiz wrote the manuscript with input from Rua Murray, Michael Plank and William Godsoe. All the authors contributed to revision.

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Contents

List of Abbreviations

ODE	**O**rdinary- **D**ifferential **E**quations
PDE	**P**artial- **D**ifferential **E**quations
IBM	**I**ndividual- **B**ased **M**odels
IDE	**I**ntegro- **D**ifferential **E**quations
1-D	**O**ne- **D**imensional (Space)
2-D	**T**wo- **D**imensional (Space)

Chapter 1

Introduction

1.1 Problem Description and Ecological Background

A key problem in ecology is to predict the presence-absence of species across a geographical region [61], [167], [199]. Dispersal is thought to have an important influence on the range limits of species, and understanding this problem in a multi-species community with priority effects is a challenging task because dispersal interacts with biotic and abiotic factors (for definitions, see Glossary section in Table (1.1)) as well as demographic stochasticity [26], [95]. We investigate the presence-absence of species by which we mean the sets of locations where a species is present or absent. We also call the boundaries of the locations at which a species is found as the range limits of species. In general, there is a suite of ecological forces that can affect the presence-absence of species: environmental factors (i.e. abiotic environments) [112], [157], [169], [173], interactions among species (i.e. biotic interactions) [23], [67], [69], [199], dispersal process [11], [13], [60], [167] and demographic stochasticity [62], [95], [171]. While various ecological forces have been considered, much remains unknown about the influences of dispersal and stochasticity on the occurrence of priority effects and species coexistence in multi-species communities. Specifically, it remains unclear what effects dispersal and stochasticity can have on the outcomes of species interactions if priority effects are important in determining presence-absence of species across heterogeneous environments. These are in fact the main concerns of this thesis.

This work is inspired by some experimental observations, which show that biotic interactions, abiotic environments [34], dispersal [37], [38], [114] and priority effects

TABLE 1.1: Glossary

Term	Description
Biotic factors	The interactions associated with living organisms (e.g. competition and predation).
Abiotic factors	The non-living environmental conditions that can affect the growth of species (e.g. temperature, salinity).
Priority effect	The situation in which the order of species becomes established affects community composition.

[130] can alter the presence-absence of species. We will briefly describe these experimental works and highlight some important insights that can be obtained from these studies. We will also use the concepts that emerge from these empirical examples to motivate our mathematical analyses in the following chapters.

Experimental Observation I - *Balanus and Chthamalus* species

In an early study, Connell [34] examined interspecific competition between different barnacle species, *Balanus and Chthamalus*, in the rocky intertidal zone along the Scottish coast. Of the two species, he observed that their vertical distribution was divided into two parts: *Chthamalus* occupied the upper region, while *Balanus* occupied the immediate region below [34].

This observation illustrates that competitive interactions and abiotic environments can affect the presence-absence of barnacle species [34]. He discovered that *Chthamalus* was limited from above by desiccation and from below by competition with *Balanus* [34]. This experimental work also illustrates that knowledge of species' environmental tolerance and biotic interactions is important to determine the presence-absence of species.

Experimental Observation II - *Drosophila* species

In a laboratory experiment, Davis et al. [37], [38] investigated the effects of biotic interactions, temperature and dispersal on the presence-absence of *Drosophila* (fruit fly) species. Their experiments consider competition between three fruit fly species, namely, *D. melanogaster*, *D. simulans* and *D. subobscura* across several temperature clines (i.e. a set of cages connected together via tubes across different temperatures, 10 ° to 25°C) [37], [38].

In comparison to single-species clines, they demonstrated that competitive interactions affect the abundances of these fruit flies in multiple-species clines [37], [38]. They also illustrated that, due to dispersal in open cline (i.e. cline in which the tubes are not blocked and these flies can move between cages), species can occupy larger temperature ranges, beyond those observed in closed cline with no-dispersal (i.e. cline in which the tubes connecting cages are blocked) [37], [38]. This finding demonstrates the potential for biotic interactions and dispersal to strongly shape species range limits across heterogeneous environments.

Experimental Observation III - *Escherichia coli.* species

It has also been demonstrated using a theoretical model [114] that the scale at which ecological processes occur can have profound impacts on coexistence and exclusion of species. To test this prediction experimentally, Kerr et al. [114] investigated competition between three *E. coli.* (bacterial) species across different environments: (i) a well-mixed environment in which ecological processes such as dispersal and interactions are non-local; (ii) an environment in which ecological processes are localised.

They found that species diversity is rapidly lost when ecological processes occur over larger distances [114] and species can coexist when these processes are localized [114], [160]. Overall, this experimental result suggests that dispersal can have different impacts on species diversity, depending on the spatial scale at which dispersal occurs.

Experimental Observation IV - *Daphnia* and *Simocephalus* species

Additionally, different experimental work using *Daphnia* and *Simocephalus* (zooplankton) species [130] support the observations that biotic interactions and environmental components such as salinity levels can determine presence-absence of species; however, in this case, the influence of priority effects mediated by intense biotic interactions is also necessary. Loureiro et al. [130] employ experimental microcosms with different salinity levels to investigate how the order in which species become established can determine the competitive outcomes of *Daphnia* and *Simocephalus* in brackish environments.

At lower salinity levels, they find that *Daphnia* or *Simocephalus* can dominate in the experimental treatments when they are given advantage in terms of establishment order [130]. When these species are inoculated simultaneously at lower salinity levels, they observe that Daphnia is a superior competitor with a higher rate of biomass increase [130]. However, it has been shown that when salinity is increased, this situation can modify species composition with competitive advantage belongs to *Simocephalus* [130]. Taken together, this observation illustrates the influential roles of priority effects and abiotic environments in structuring community assembly.

A consistent observation in these experimental studies is that biotic interactions are one of the important factors in determining the presence-absence of species across heterogeneous environments. Ecologically, a species has a range of locations (or environments) where it is able to occupy in the absence of biotic interactions (i.e. fundamental niche) [100]. However, when confronted with other species, this excludes each species from some locations and they can occupy a more narrow portion of their fundamental ranges (i.e. realised niche) [100], [140]. As discussed above, Connell's experimental work [34] on barnacle species provides a good illustration of these concepts: when Connell removed *Balanus* from the lower intertidal zone, *Chthamalus* replaced it; due to competition from *Balanus*, the realised niche for *Chthamalus* was smaller than its fundamental niche.

In general, the strength of biotic interactions can determine community dynamics, with coexistence of species being possible in some situations [23], [167]. Note that in ecological literature, the term "coexistence" has different interpretation depending on the spatial scale of observation. At a small spatial scale, multiple species can coexist at a single location (i.e. local coexistence) as a result of weak biotic interactions [69], [70]. When biotic interactions are relatively intense, priority effects can occur, with species range limits depend on initial abundances [23], [70]. In this case, observation at a local scale would show that only one species can persist at any given location, with local coexistence is impossible [70]. However, if we make an observation at larger spatial scales by combining several locations into a single observation, we would find that regional coexistence is possible [70]. *In this thesis, we use the term coexistence to mean local coexistence, in which multiple species can coexist at the same location.*

As discussed above, priority effects can arise due to intense biotic interactions. This phenomenon has been shown to determine community assembly in various ecological systems [23], [167], for instance, in a system of two interacting flour beetles [154], [155], in a small food web community incorporating competition and predation [66] and in plant [110] and plankton [130] communities. These studies illustrate that priority effects generally depend on history of arrival or high initial abundances of species [66]. Experimental studies have manipulated initial abundances or the establishment order of species to explore the occurrence of priority effects [154], [155]. Other experimental studies using a microbial community [47] demonstrate that variation in the timing of species introduction can lead to different community assembly. Additionally, some studies observe that priority effects can also be influenced by abiotic environments. Experimental work using *Daphnia* species [130] discussed before find that abiotic components such as salinity levels can affect community dynamics and thus may alter priority effect outcomes. Experimental studies of Park [154], [155] also show how important such an interaction between biotic factor and abiotic environments (e.g. temperature and humidity) in determining the occurrence of priority effects.

Local dispersal (i.e. dispersal process that occurs between adjacent locations) also plays an important role in structuring community assembly [37], [38], [167]. However, how dispersal shapes community assembly has proven difficult to understand, because dispersal can have contrasting effects on species presence-absence [19]. On the one hand, dispersal can allow species to be present in otherwise unsuitable environments, as shown by the experimental studies of Davis et al. [37], [38] discussed above. In an ecological community, dispersal can increase species diversity by immigration of species from other locations [19]; it has been shown that sink populations (i.e. low quality habitat with few individuals) can only persist if they receive sustained dispersal from source populations (i.e. high quality habitat with more abundant individuals) [9], [82], [122]. Dispersal can also facilitate local coexistence of species across heterogeneous environments as a consequence of source-sink dynamics [9]. On the other hand, the inclusion of dispersal into ecological systems with intense biotic interactions can be detrimental to species coexistence [9], [128]. While moderate dispersal levels can enhance species diversity by alleviating local competitive exclusion, rapid dispersal can

reduce diversity by amplifying the effect of competition from other species [136]. It has also been demonstrated that increasing dispersal rate above a threshold value can lead to exclusion of species [9]. The same phenomenon is also observed in the study of competition between two-species involving priority effects [126]: species coexistence is no longer possible as dispersal intensity increases above a threshold dispersal rate.

Given these contrasting observations of dispersal, it remains unclear how dispersal process that occurs at larger spatial scales (i.e. non-local dispersal process), in interaction with other ecological forces, shapes a multi-species community assembly with priority effects. Several studies have investigated the influences of different modes of dispersal (i.e. local and non-local dispersal) in shaping community dynamics in the presence of biotic interactions [18], [92], [114], [152]. Experimental work of Kerr et al. [114] discussed above demonstrates the critical influence of dispersal distance in promoting species diversity; it has been shown that short-range dispersal can promote species coexistence, whereas long-range dispersal leads to exclusion of species. Similar observations are also realised in other experimental studies [18], [19], in which species diversity is reduced when dispersal process occurs over larger spatial scales. In contrast to the aforementioned observations, Etienne et al. [49] illustrate that the establishment and persistence of species are determined by the modes of dispersal, where non-local dispersal can promote species survival. Whether dispersal affects community dynamics positively or negatively may depend on the spatial scale of dispersal process [18] and its interaction with other ecological forces [26], [95], but these possibilities have received less attention and remain to be explored by experimental and theoretical studies.

Here, we use mathematical modelling to investigate how species establishment order, stochasticity and dispersal interact to determine where a species will be present. In particular, we first employ a deterministic model, which describes an example of biotic interactions, namely competition between species across heterogeneous environments. These biotic and abiotic forces have been demonstrated to be essential ecological forces in shaping the presence-absence of species [23]. To do this, we extend previous deterministic theoretical studies involving two-species [133], [164] to model competition among multiple species along an environmental gradient (i.e. corresponds

to environmental suitability, in which the suitability of a particular environment is represented by a carrying capacity term). This extension leads to a system of ordinary differential equations (ODE) consisting of biotic interactions and environmental suitability terms for multiple species. By employing this model, we investigate the joint effects of biotic and abiotic factors on community dynamics. In particular, we explore the consequences of biotic interactions on competitive outcomes across heterogeneous environments.

To investigate the effects of local dispersal on the outcomes of species interactions, we incorporate a diffusion term [29], [107], [118] into our deterministic models with biotic interactions and environmental suitability; this leads to a system of partial-differential equations (PDE). This investigation is motivated by different studies of two-species systems [23], [69], [70], which show that local dispersal and biotic interactions can affect the range limits of species. It has been illustrated that species coexistence (respectively, priority effects) occur in the presence of weak (respectively, aggressive) competitive interactions. In the case of priority effects, the range limits of species depends on initial abundances and dispersal intensity [23]. By using this information from two-species models, we examine the conditions under which priority effects occur and disappear as local dispersal strength changes in a multi-species community.

Another objective of this thesis is to explore the impact of stochasticity on the dynamics of multi-species communities. Motivated by our population-level deterministic models, we develop a comparable stochastic individual-based model (IBM) that captures the dynamics at an individual scale. Our aim is to check whether the range-limit predictions are similar using the stochastic and deterministic models. We also want to examine the occurrence of priority effects in our stochastic IBM by considering various dispersal intensity and different population sizes. This investigation is driven by some studies [120], [198], which show that even simple stochastic models can result in dynamical behaviour that contrasts with the predictions of deterministic models. It has also been highlighted in empirical studies [26] that priority effects are more likely to appear in systems with large populations and lower migration rates. This phenomenon

has been demonstrated to result from the interaction of stochastic process (e.g. colonisation) and species establishment order, which can lead to alternative community compositions [26]. Based on this information, we expect that the occurrence of priority effects in the stochastic models depends on population size and also the strength of local dispersal.

While the assumption of local dispersal in modelling an ecological system can be applied to some animal and plant species that can disperse over short distances [20], [147], it may not be relevant to other species that can transport their offsprings larger distances via dispersal vectors such as animals, wind and water [20], [86], [98], [147], [148]. These observations lead to the development of a deterministic model with non-local dispersal (i.e. integro-differential equations (IDE)) in this thesis. By employing different dispersal models, we explore the effects of non-local dispersal process on the occurrence of priority effects in comparison to a local dispersal process. Additionally, we investigate the impacts of different modes of dispersal on species coexistence in multi-species communities. We also aim to provide theoretical explanations for the effects of dispersal on priority effects in multi-species communities.

Despite the development of numerous ecological systems and different modelling approaches to investigate the joint influences of dispersal, biotic and abiotic components on community dynamics, some of them are still analysed using one-dimensional (1-D) space models [21], [69], [70], [133], [164]. From a methodological viewpoint, an important problem is to establish how such 1-D estimation of the two-dimensional (2-D) space systems affects the predictions of community dynamics [144]. To investigate this problem, we extend our 1-D PDE to the 2-D space systems. By employing these two models, we want to develop an understanding of when the ecological predictions are similar, with respect to the occurrence of priority effects and species coexistence in multi-species communities.

1.2 Outline of the Thesis

This thesis is outlined as follows. In Chapter 2, we provide a general overview of selected models of population dynamics and dispersal process. We outline:

- Derivation of several deterministic growth models from stochastic birth-death process.
- Modelling single-species population dynamics via exponential and logistic growth models.
- Modelling biotic interactions using population dynamics models.
- The linear stability analysis of a model with biotic interactions is performed and several ecological implications on the dynamics of species interactions are discussed.
- Derivation of diffusion models from stochastic random walk process.
- Modelling dispersal process via local dipersal (using a diffusion model) and non-local dispersal (using an integro-differential equation model).
- Previous works and developments of modelling frameworks related to this study are also presented.

In Chapter 3, we develop a deterministic model of range limits for multiple species. The model is a spatially extended ODE, which becomes a system of partial-differential equations (PDE) with addition of diffusion. Here, we aim to investigate the joint influences of biotic interactions and abiotic environments on the range limits of multiple species using the ODE model. To do this, we develop some results:

- The analytical results on range limits of species and numerical evidences are presented to illustrate the possible outcomes of the models, particularly coexistence of species and priority effects.
- Some biological mechanisms that can significantly shift species range limits are discussed.
- In the case of priority effects, the dependence of species interactions outcomes on initial abundances is discussed. In particular, competitive exclusion of all but one species is observed. A biological control strategy is proposed based on the findings of this chapter.

In Chapter 4, we examine the effects of local dispersal on community assembly using a PDE model. We show that:

- Local dispersal substantially expands species ranges in the presence of biotic and abiotic components. Consequently, this situation enhances the spatial extent of multi-species coexistence compared to no-dispersal case.
- Dispersal weakens competitive exclusion effects that occur in no-dispersal case and allows coexistence of multiple species.
- The existence of threshold values of competitive strength (i.e. transcritical bifurcations) are established in the models with and without dispersal by employing numerical continuation. These bifurcations result in different species presence-absence and the occurrence of priority effects.

In Chapter 5, we further investigate the impact of local dispersal on priority effects. Our analysis shows conditions under which priority effects occur and disappear as dispersal intensity changes. In particular, we demonstrate:

- For moderate migration levels, dispersal enhances priority effects and promotes coexistence of species.
- Increasing dispersal strength leads to the reduction of priority effects; consequently, strong dispersal causes extinction of some species.

Additionally, in Chapter 5, we examine the combined impacts of stochasticity and local dispersal on the occurrence of priority effects using stochastic individual-based models (IBM). We will demonstrate the following observations:

- While priority effects are more prevalent in the stochastic IBM than in the deterministic (PDE) models for large populations, fewer occurrences of priority effects are observed in the small-population IBM.
- We show that priority effects are eliminated by weaker values of dispersal when population sizes are small than when they are large.

In Chapter 6, we incorporate a non-local dispersal process into our multi-species community models. This inclusion leads to a system of integro-differential equations (IDE). By using the IDE and PDE models, we explore the effects of different dispersal patterns on the predictions of priority effects and species coexistence. We will illustrate the following observations:

- Priority effects are more pronounced in the non-local dispersal models than in the local dispersal models.
- Computations using numerical continuation methods show the existence of transcritical and saddle-node bifurcations in both models. These bifurcations determine the occurrence of priority effects in this multi-species community.
- Our two-parameter continuation result shows that there is a co-dimension 2 point, corresponding to a degenerate transcritical bifurcation: at this point, the transcritical bifurcation changes from subcritical to supercritical with corresponding creation of a saddle-node bifurcation curve.
- Dispersal also has contrasting effects on coexistence of species: although very long-range dispersal can result in exclusion of species, intermediate-range dispersal can permit multi-species coexistence in comparison to short-range dispersal (or purely local dispersal).

In Chapter 7, we extend our 1-D space PDE models in Chapter 5 to two spatial dimensions. By comparing simulation results from the 2-D space models with the 1-D space models, we show that:

- Adding another spatial dimension modifies the strength of priority effect. The occurrence of priority effects are either qualitatively similar in both models, or they are strengthened or weakened, depending on the differences in species environmental suitability and magnitude of dispersal.
- We observe that increasing environmental dimensionality of the models promotes multi-species coexistence.

Finally, in Chapter 8, we conclude by summarising several important insights from this thesis, and then suggest some possible aspects for future work.

1.3 Thesis Publication

A paper presenting the results for the partial differential equations and stochastic individual-based models, from Chapter 5, has been published by Ecological Modelling [141].

Chapter 2

Overview of Selected Mathematical Models

2.1 Introduction

This thesis investigates the presence-absence of species using deterministic and stochastic models. We first review several aspects of these modelling frameworks and introduce the notations that will be used throughout this thesis. To begin, we model single-species population dynamics using stochastic birth-death process and present their deterministic counterparts, exponential and logistic growth models. We then discuss models of biotic interactions and show how mathematical methods such as stability analysis and phase portraits can be used to analyse these models. After we have discussed species population dynamics, we model the dispersal process using stochastic random walk theory; in particular, we discuss the derivation of a deterministic diffusion equation from this theory. In general, diffusion model describes a local dispersal process whereby a species is assumed to move between adjacent spatial locations following random walks. To illustrate another pattern of dispersal, we present a non-local dispersal model, which describes dispersal process that occurs over non-adjacent or larger spatial ranges. We also discuss several applications of the aforementioned population dynamics and dispersal models in ecology and other fields. We refer the reader to standard text books on mathematical modelling [118], [161], [194] for further details and discussion.

2.2 Modelling Single-species Population Dynamics

In this section, we focus our attention on the growth process for a single-species. First, we consider the growth of individuals due to demographic stochasticity e.g. birth and death events. Then, we discuss two fundamental deterministic growth models, namely exponential and logistic growth models.

2.2.1 Stochastic Processes

Linear Birth-Death Process

We define the underlying stochastic process by:

$$\begin{aligned} n(t) &= \text{Number of individuals at time } t \\ p_k(t) &= Pr\{n(t) = k\}, \qquad k = 0, 1, 2, ... \end{aligned}$$

Let us start with the linear birth and death processes where we assume that individual birth rate, b, and death rate, d, remain constant, independent of population size. Following this assumption, the probability that an individual from a species gives birth in a small time interval $[t, t + \Delta t)$ is given by $b\Delta t$ and the probability it dies is given by $d\Delta t$. Thus, the transition probabilities for k individuals in a small time step Δt are given by:

$$\begin{aligned} Pr\{\text{1 birth in } [t, t + \Delta t)\} &= bk\Delta t + o(\Delta t) \\ Pr\{\text{1 death in } [t, t + \Delta t)\} &= dk\Delta t + o(\Delta t) \\ Pr\{\text{no event in } [t, t + \Delta t)\} &= 1 - k(b + d)\Delta t + o(\Delta t) \end{aligned}$$

and the probability of more than one birth or death is $o(\Delta t)$. We can derive a differential equation from this stochastic process. The master equation (i.e. the equation that describes the time evolution of the probability distribution of states) that can describe

this process is [161], [194]:

$$p_k(t+\Delta t) = b(k-1)\Delta t p_{k-1}(t) + d(k+1)\Delta t p_{k+1}(t) + (1-(b+d)k\Delta t)p_k(t) + o(\Delta t) \tag{2.1}$$

Dividing (2.1) by Δt and letting Δt tends to zero, we obtain the set of differential equations:

$$\frac{\mathrm{d}}{\mathrm{d}t}p_k(t) = b(k-1)p_{k-1}(t) - (b+d)kp_k(t) + d(k+1)p_{k+1}(t) \tag{2.2}$$

over $k = 0, 1, 2, ...$ and $p_{-1} = 0$. In order to proceed, we introduce the moment generating function (mgf), which is a function that generates the moments of the random variable associated with the mgf. Let us denote the mgf as $M(\theta, t)$:

$$M(\theta, t) = \sum_0^\infty e^{\theta k} p_k(t) \tag{2.3}$$

If we differentiate equation (2.3) with respect to time and make use of the differential equations of (2.2), we get:

$$\begin{aligned}
\frac{\partial M}{\partial t} &= \sum_0^\infty e^{\theta k}\frac{\partial p_k}{\partial t} \\
&= \sum_0^\infty e^{\theta k}[b(k-1)p_{k-1} - (b+d)kp_k + d(k+1)p_{k+1}] \\
&= be^{\theta}\sum_0^\infty ke^{\theta k}p_k - (b+d)\sum_0^\infty ke^{\theta k}p_k + de^{-\theta}\sum_0^\infty ke^{\theta k}p_k \\
&= \sum_0^\infty ke^{\theta k}p_k[be^{\theta} - (b+d) + de^{-\theta}]
\end{aligned} \tag{2.4}$$

Notice that $\frac{\partial M}{\partial \theta} = \sum_0^\infty k e^{\theta k} p_k$. Then we can arrive at the partial-differential equation:

$$\frac{\partial M}{\partial t} = [b(e^\theta - 1) + d(e^{-\theta} - 1)]\frac{\partial M}{\partial \theta} \tag{2.5}$$

This differential equation can be used to derive differential equation satisfied by the mean of this stochastic process. Let us differentiate (2.5) with respect to θ, to get:

$$\frac{\partial^2 M}{\partial t \partial \theta} = [be^\theta - de^{-\theta}]\frac{\partial M}{\partial \theta} + [be^\theta + de^{-\theta} - (b+d)]\frac{\partial^2 M}{\partial \theta^2}] \tag{2.6}$$

Evaluating equation (2.6) at $\theta = 0$ and using the fact that:

$$\frac{\partial^j M}{\partial \theta^j} = E[n^j(t)], \text{at } \theta = 0 \tag{2.7}$$

we obtain the differential equation for the mean, $E[n(t)]$. Let us denote $z(t) = E[n(t)]$ to get:

$$\frac{\mathrm{d}}{\mathrm{d}t} z(t) = (b-d)z(t) \tag{2.8}$$

Applying the initial condition $z(0) = z_0$ (where z_0 is the initial abundances of species at time $t = 0$), we have the solution:

$$z(t) = z_0 e^{(b-d)t} \tag{2.9}$$

Equation (2.9) has the same form of the deterministic exponential growth model [161], [194]:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = (b-d)N(t), \quad N(0) = N_0 \tag{2.10}$$

with the deterministic solution:

$$N(t) = N_0 e^{(b-d)t} \tag{2.11}$$

The equation (2.9) given by the stochastic process is equivalent to the deterministic solution (2.11).

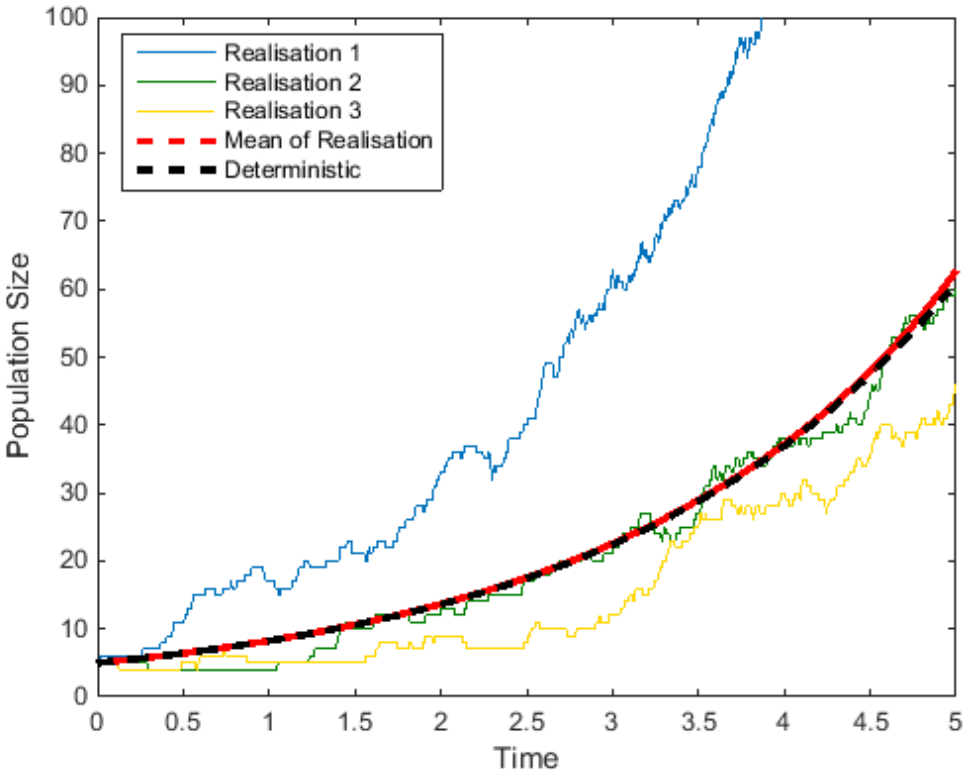


FIGURE 2.1: The stochastic linear birth and death processes (over 5000 simulations) with birth rate, $b = 1$, death rate, $d = 0.5$, and initial condition $z_0 = 5$. Solid blue, green and yellow curves indicate the possible paths until time $t = 5$; dotted red curve indicates the mean of realisation, which corresponds to the estimate of the solution of equation (2.9); solid black curve corresponds to the deterministic solution of an exponential growth model (2.11)

Figure 2.1 illustrates an example of a stochastic simulation of the linear birth-death process. We notice that the trajectories of individual realisations (solid blue, green and yellow curves) can be different from the deterministic solution (dotted black curve). The mean of stochastic realisations (dotted red curve) are in agreement with the solution of an exponential growth model (dotted black curve).

Non-linear Birth-Death Process

Having studied the linear birth-death process, this stochastic process may be made more realistic by incorporating density-dependent (i.e. nonlinear death process). Motivated by the logistic growth process [161], [194], we can let the death rate depends on the population size to prevent unlimited exponential growth as shown by Figure 2.1. To model this stochastic process, let the per capita birth rate be b, the per capita death rate be d, the intrinsic growth rate be r and some constant K. Comparing with the logistic model [161], [194], the birth rate is $b = r$ and the death rate is $d = \frac{rn}{K}$. The possible types of transition: birth (with probability $bn\Delta t + o(\Delta t)$); death (with probability $dn\Delta t + o(\Delta t)$); or no event occurs (with probability $1 - (b + d)n\Delta t + o(\Delta t)$).

Similar to equation (2.2), we can derive the differential equation for this stochastic process:

$$\frac{\mathrm{d}}{\mathrm{d}t}p_n(t) = r(n-1)p_{n-1}(t) + \frac{r}{K}(n+1)^2 p_{n+1}(t) - rn(1+\frac{n}{K})p_n(t) \tag{2.12}$$

over $n = 0, 1, 2, ...$ and $p_{-1} = 0$. Applying the moment generating function technique (i.e. similar steps as in equation (2.3)- (2.5)), we can arrive at the following partial differential equation satisfied by the mgf for this stochastic process:

$$\frac{\partial M}{\partial t} = [r(e^{\theta} - 1)\frac{\partial M}{\partial \theta} + \frac{r}{K}(e^{-\theta} - 1)]\frac{\partial^2 M}{\partial \theta^2} \tag{2.13}$$

Differentiating (2.13) with respect to θ, to get:

$$\frac{\partial^2 M}{\partial t \partial \theta} = r(e^{\theta} - 1)\frac{\partial^2 M}{\partial \theta^2} + re^{\theta}\frac{\partial M}{\partial \theta} + \frac{r}{K}(e^{-\theta} - 1)\frac{\partial^3 M}{\partial \theta^3} - \frac{r}{K}e^{-\theta}\frac{\partial^2 M}{\partial \theta^2} \tag{2.14}$$

Evaluating equation (2.14) at $\theta = 0$ and using equation (2.7), we can get the differential equation for the mean of this stochastic process, $z(t)$ [5]:

$$\frac{\mathrm{d}}{\mathrm{d}t}z(t) = rz(t) - \frac{r}{K}E[z^2(t)] \tag{2.15}$$

Notice that the equation (2.15) cannot be solved for $z(t)$ since the differential equation depends on the higher-order moment e.g. $E[z^2(t)]$. The equation for $E[z^2(t)]$ will also depend on the third-order moment and so on. The system is not "closed". If we make the mean-field assumption (i.e. individuals are assumed to be well-mixed in homogeneous environment, and they interact with one another in proportion to their average density) [44], then $E[z^2(t)] = E[z(t)]^2 = z^2(t)$. In this case, the equation (2.15) can be the same as the deterministic logistic growth equation:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN - \frac{r}{K}N^2 \tag{2.16}$$

Figure 2.2 shows the stochastic simulation for the birth and density-dependent death process and the deterministic logistic growth model. We can see that the mean of stochastic realisations (dotted red curve) are in agreement with the solution of the logistic growth model (solid black curve).

Applications of Stochastic Birth-Death Models

The stochastic birth-death model has been applied in various ways in ecology [140]: birth-death models are employed to explore the extinction phenomenon, particularly for species at small population size; in the theory of island biogeography, the stochastic birth-death models are used in exploring the ability of species to colonise islands;

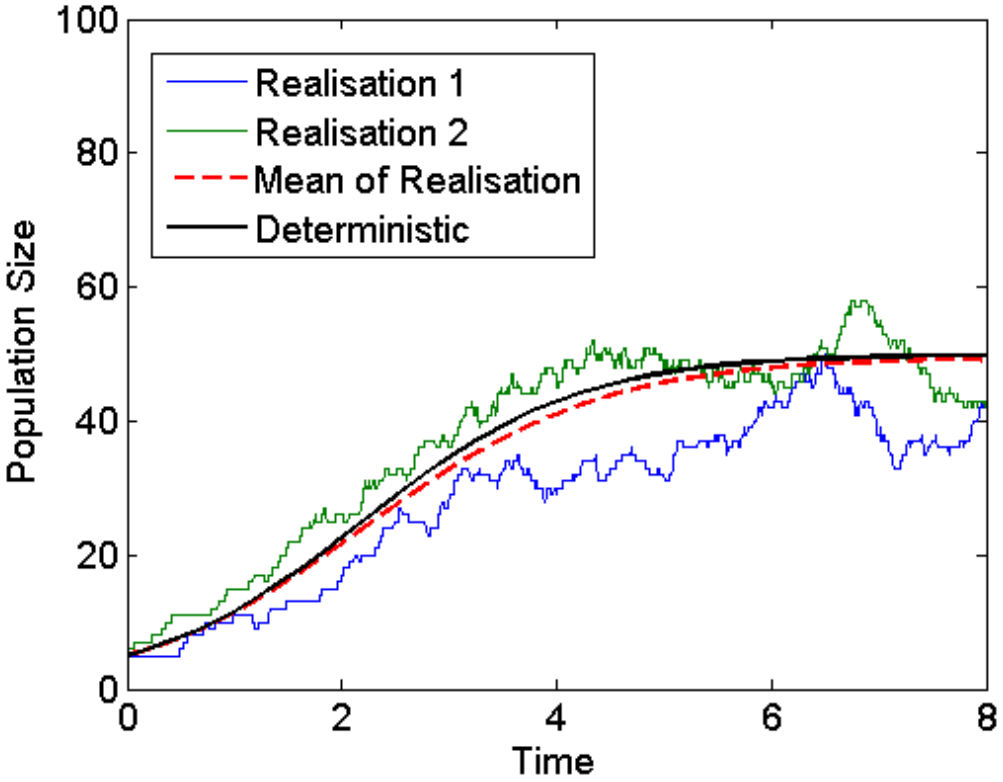


FIGURE 2.2: The stochastic simulation (over 10 000 simulations) for the birth and density-dependent death process, with $r = 1$, $K = 50$, and initial condition $z_0 = 5$. Solid blue and green curves indicate two sample realisations until time $t = 8$; dotted red curve indicates the mean of realisation, which corresponds to the estimate of the solution of equation (2.15); solid black curve corresponds to the deterministic solution of the logistic growth model (2.16).

in metapopulation theory, birth-death models have been used to estimate extinction probabilities/rates caused by demographic stochasticity.

2.2.2 Deterministic Growth Processes

An Exponential Growth Model

Now, we discuss the deterministic growth process i.e. the exponential model. The exponential model assumes that the growth rate of species is proportional to the current population size. This assumption leads to species population density to grow exponentially as time increases. The mathematical description of the exponential growth

model is as follows [107], [161], [194]:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN(t), \;\; N(0) = N_0 \tag{2.17}$$

where the rate of change describes the temporal evolution of the population density N with r is the intrinsic growth rate of species. This rate corresponds to the proportional increase of the population size N per unit of time. The solution of this differential equation is given by:

$$N(t) = N_0 e^{rt} \tag{2.18}$$

which describes the population growth process over time starting with initial species density of N_0. The time series plot of the exponential growth model is shown in Figure 2.1 (dotted black curve) as an example. As time increases, the population will grow without bound, which is the drawback of exponential model.

Logistic Growth Model

Exponential growth is not physically realistic as species population cannot grow without bound. To correct this behaviour, the logistic growth model was proposed by Verhulst [192] in 1845. In general, the logistic model assumes that the growth rate of species is influenced by both current population size and the availability of resources. Biologically, these assumptions indicate that the growth process of species is bounded due to limitation of resources (e.g. food, living areas) in nature. The logistic model is given by the following equation [107], [161], [194]:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(1 - \frac{N}{K}\right) \tag{2.19}$$

where N is the population density of species, r is the intrinsic growth rate and K is the carrying capacity of the environment (i.e. an upper bound for population size). Solving

equation (2.19), we obtain the following solution:

$$N(t) = \frac{N_0 K e^{rt}}{K + N_0(e^{rt} - 1)}, \quad N(0) = N_0 \tag{2.20}$$

which describes the temporal dynamics of logistic growth process with initial species density of N_0, as shown by Figure 2.2 (dotted black curve), as an example. For positive values of r, the population density converges to K as $t \to \infty$.

Applications of Deterministic Growth Models

The exponential and logistic growth models have been validated in numerous ecological studies [140]. One of the most famous examples was the introduction of European rabbits to Australia in 1859 in which these rabbits grew rapidly according to an exponential growth [140]. The growth of burrowing mayflies in Lake Erie also shows an exponential growth process from 1991-1997 [134]. Another example of species that demonstrates an exponential growth process is monk parakeet species in the United States [187]. In the case of logistic model, an early laboratory work by Gause [63] showed that the growth of *Paramecium caudatum* was consistent with a logistic curve. Additionally, the observed population size of harbour seals in Washington also shows a logistic growth process from 1978-1999 [102]. Another example of species that follows logistic growth process is willow species [7].

2.3 Modelling Biotic Interactions Between Species

So far we have discussed the population dynamics of a single-species. But what happens if this species meets with other species? Interactions between species are called biotic interactions. By using the deterministic model with biotic interactions (e.g. competition), we examine the possible outcomes e.g. coexistence of species, exclusion of species and priority effects. We refer the reader to [24], [72], [118], [140] for further details and discussion on this matter.

2.3.1 Two-Species Competition Model

In the 1920s and 1930s, A.J. Lotka [129] and V. Volterra [193] developed a competition model for two species that is the framework for competition studies in ecology [140]. The model is outlined as below:

$$\frac{\partial N_i}{\partial t} = \frac{r_i N_i}{K_i}\left(K_i - \sum_{j=1}^{m} \alpha_{ij} N_j\right) \qquad (i = 1, 2, ..., m) \tag{2.21}$$

where N_i is the density of species i, r_i is the intrinsic growth rate of species i, K_i is the carrying capacity and α_{ij} is the competitive effect of species j on species i. By rescaling the density of species i relative to its intraspecific competition coefficient α_{ii}, we may effectively set the intraspecific competition coefficients α_{ii} to equal 1, and the remaining competition coefficients α_{ij} represent the ratio of intraspecific to interspecific competition. A standard dynamical system analysis for two-species (e.g. $m = 2$) [72], [118], [178] demonstrates that there are several possible outcomes of the model (2.21), depending on the competition coefficients α_{12} and α_{21} and the ratio of the carrying capacities $\frac{K_1}{K_2}$. We present the stability analysis of the two-species model in the next section and discuss the possible outcomes of species interactions.

Stability Analysis

For the two-species system ($m = 2$), the steady state can be calculated by setting the time-derivative in the model (2.21) to zero. In particular, the steady states (N_1^*, N_2^*) satisfy the system of equations:

$$\frac{r_i N_i}{K_i}\left(K_i - \sum_{j=1}^{m} \alpha_{ij} N_j\right) = 0 \qquad (i = 1, 2) \tag{2.22}$$

For the first of these equations ($i = 1$), we can have either $N_1^* = 0$ or $N_1^* = K_1 - \alpha_{12} N_2^*$ while for the second we can have either $N_2^* = 0$ or $N_2^* = K_2 - \alpha_{21} N_1$. Following this way, we can proceed in four cases, substituting each solution of the first equation

into the solution for the second equation. So, we can have four steady states namely $(0,0)$, $(K_1,0)$, $(0,K_2)$ and:

$$(N_1^*, N_2^*) = \left(\frac{K_1 - \alpha_{12}K_2}{1-\alpha_{12}\alpha_{21}}, \frac{K_2 - \alpha_{21}K_1}{1-\alpha_{12}\alpha_{21}} \right)$$

Because of biological significance, we restrict our attention to (N_1^*, N_2^*) that lies in positive quadrant for certain choices of parameters.

The Jacobian matrix for the model (2.21) with $m = 2$ is

$$J(N_1^*, N_2^*) = \begin{pmatrix} r_1 - 2\frac{r_1}{K_1}N_1^* - \frac{r_1\alpha_{12}}{K_1}N_2^* & -\frac{r_1\alpha_{12}}{K_1}N_1^* \\ -\frac{r_2\alpha_{21}}{K_2}N_2^* & r_2 - 2\frac{r_2}{K_2}N_2^* - \frac{r_2\alpha_{21}}{K_2}N_1^* \end{pmatrix} \tag{2.23}$$

In order to determine whether or not each of these steady states is stable, we compute the eigenvalues of the Jacobian matrix evaluated at that steady state. For the point $(0,0)$, we have:

$$J(0,0) = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix} \tag{2.24}$$

with eigenvalues r_1 and r_2. Since r_1 and r_2 are both assumed positive, we can conclude that this steady state is repelling.

For the steady state $(K_1,0)$, the Jacobian matrix is

$$J(K_1,0) = \begin{pmatrix} -r_1 & -r_1\alpha_{12} \\ 0 & r_2 - \frac{r_2\alpha_{21}}{K_2}K_1 \end{pmatrix} \tag{2.25}$$

where the eigenvalues are $-r_1$ and $r_2(1-\alpha_{21}\frac{K_1}{K_2})$. In this case, the steady state is a saddle for $\alpha_{21}K_1 < K_2$ and attracting for $\alpha_{21}K_1 > K_2$.

For the steady state $(0, K_2)$, the Jacobian matrix is

$$J(0, K_2) = \begin{pmatrix} r_1 - \frac{r_1 \alpha_{12}}{K_1} K_2 & 0 \\ -r_2 \alpha_{21} & -r_2 \end{pmatrix} \tag{2.26}$$

where the eigenvalues are $r_1(1 - \alpha_{12}\frac{K_2}{K_1})$ and $-r_2$. Based on these eigenvalues, the steady state is a saddle for $\alpha_{12}K_2 < K_1$ and attracting for $\alpha_{12}K_2 > K_1$.

For the two-species steady state (N_1^*, N_2^*), the stability of the model (2.21) can also be evaluated [24], [72], [97], [118]. In brief, this steady state is attracting if $\alpha_{12} < \frac{K_1}{K_2} < \frac{1}{\alpha_{21}}$, and a saddle otherwise.

Ecological Considerations

Based on the stability analysis, there are several cases of competitive outcomes that we can consider. From an ecological viewpoint, we classify the four cases as follows:

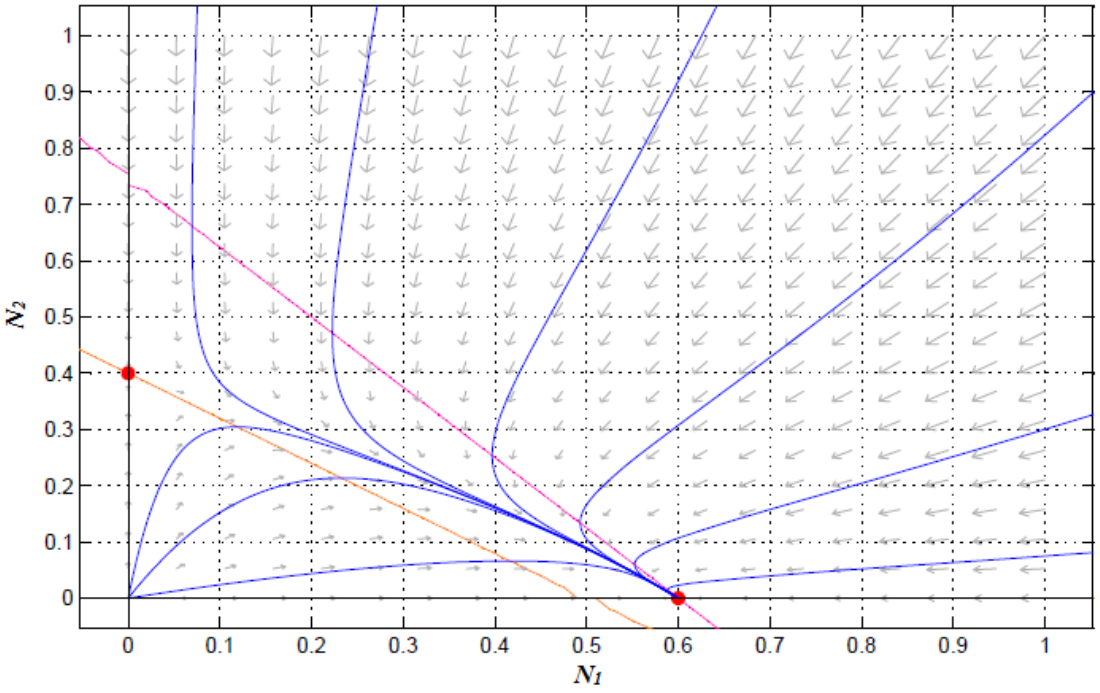


FIGURE 2.3: Phase portrait for Case (i) ($\frac{K_1}{K_2} > \alpha_{12}, \frac{1}{\alpha_{21}}$). Parameter values: $\alpha_{12} = \alpha_{21} = 0.8$; $K_1 = 0.6$, $K_2 = 0.4$; $r_1 = r_2 = 1$. Initial conditions: $N_1 = N_2 = 0.01$

Case (i): Species 1 excludes species 2 ($\frac{K_1}{K_2} > \alpha_{12}, \frac{1}{\alpha_{21}}$)

Case (ii): Species 2 excludes species 1 ($\frac{K_1}{K_2} < \alpha_{12}, \frac{1}{\alpha_{21}}$)

For Case (i), species 2 has a relatively small effect on species 1 and species 1 has a relatively large effect on species 2. This situation leads to exclusion of species 2 by species 1 (with the steady state approaches its carrying capacity), and shows an example where two-species coexistence state is not in positive quadrant. This outcome is depicted by Figure 2.3. From an ecological viewpoint, this case corresponds to Gause's competitive exclusion principle [64], which proposes that coexistence are impossible when two species compete for the same limited resource. If the inequality is reversed, the competitive outcome is also reversed as in Case (ii). In this case, species 2 excludes its competitor and approaches carrying capacity. Similar phase portrait as shown by Figure 2.3 could be plotted for Case (ii).

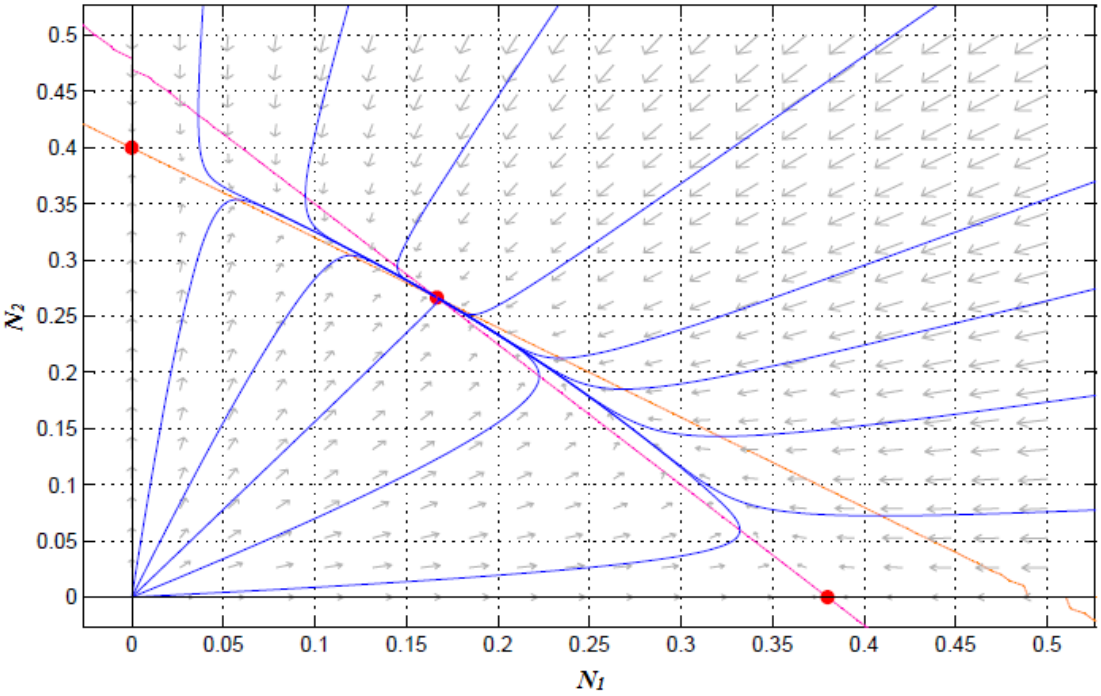


FIGURE 2.4: Phase portrait for Case (iii) ($\alpha_{12} < \frac{K_1}{K_2} < \frac{1}{\alpha_{21}}$). Parameter values: $\alpha_{12} = \alpha_{21} = 0.8$; $K_1 = 0.38$, $K_2 = 0.4$; $r_1 = r_2 = 1$. Initial conditions: $N_1 = N_2 = 0.01$

Case (iii): Coexistence of species ($\alpha_{12} < \frac{K_1}{K_2} < \frac{1}{\alpha_{21}}$)

When interspecific competition of both species are relatively weak (i.e. $\alpha_{12}\alpha_{21} < 1$), coexistence of species are possible, as shown by Figure 2.4. The single-species steady states (upper and lower red circles) are both unstable saddle points, so the trajectories converge to a two-species steady state (middle red circle), which is a stable node.

Case (iv): Priority effects ($\frac{1}{\alpha_{21}} < \frac{K_1}{K_2} < \alpha_{12}$)

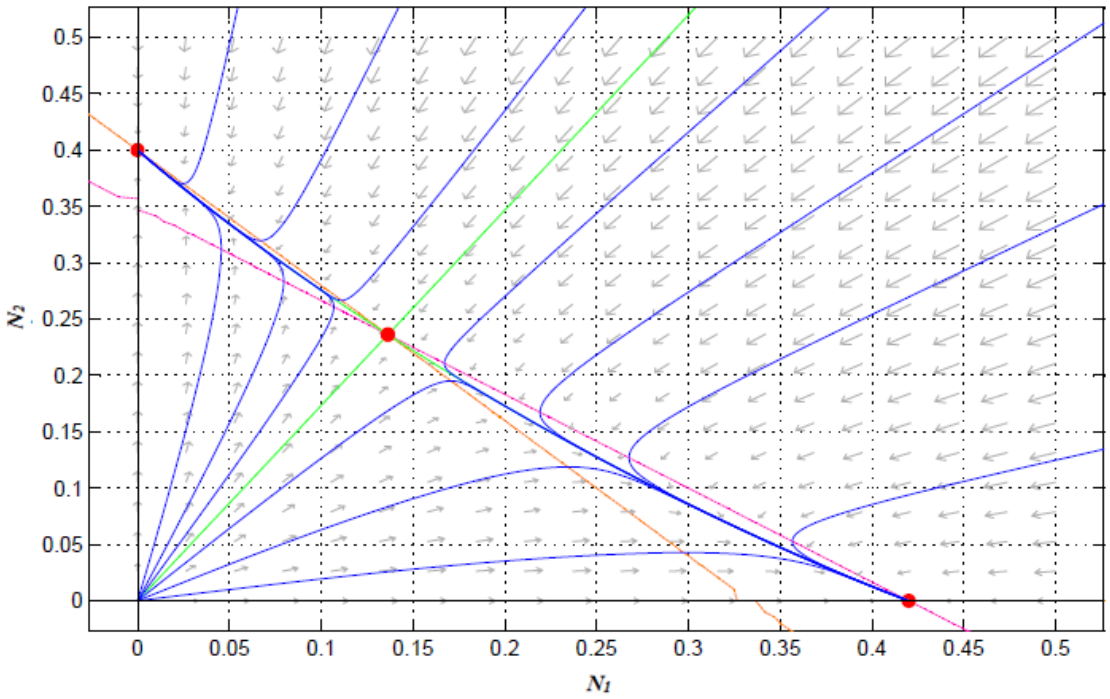


FIGURE 2.5: Phase portrait for Case (iv) ($\frac{1}{\alpha_{21}} < \frac{K_1}{K_2} < \alpha_{12}$). Parameter values: $\alpha_{12} = \alpha_{21} = 1.2$; $K_1 = 0.42$, $K_2 = 0.4$; $r_1 = r_2 = 1$.

Based on Figure 2.5, if the interspecific competition for both species are relatively intense (i.e. $\alpha_{12}\alpha_{21} > 1$), then the single-species steady states (upper and lower red circles) are both stable nodes. The two-species steady state (middle red circle) is a saddle point and it lies in between the two nodes. The basin boundary (i.e. the stable manifold of this saddle point (green line)) separates the basins for these two nodes. In this case, either species can competitively exclude the other, depending on initial abundances.

Applications of Deterministic Models with Biotic Interactions

By employing Lotka-Volterra competition model, Gause [63] was able to predict the outcomes of competition between two *Paramecium* species in an experimental setup; the model predictions were in agreement with the experimental results. This model has also been illustrated to adequately describe the distributions of competing protozoan species[190]. Additionally, Lotka-Volterra type model [9] is also used to study the empirical observations of competition between parasite species of the butterfly *Melitaea cinxia* [122]. As discussed above, one of the outcomes of Lotka-Volterra competition model is species coexistence, which occurs when biotic interactions are relatively weak: desert granivores such as ants and rodents who eat seeds provide a good example to this case; both can coexist in North American deserts consuming seeds as their main source of food [106]. It has also been observed that similar bird species in some small islands in New Guinea often fail to coexist with each another [106]. These islands are occupied by one or the other competing bird species, which is what would be anticipated if interspecific competition is stronger than intraspecific competition [106].

2.4 Modelling Dispersal Process

We now discuss species dispersal models, namely local dispersal and non-local dispersal models.

2.4.1 Local Dispersal Models

We begin by modelling the dispersal of an individual using stochastic random walk theory. This theory can be used to establish the relationship between random walks as a description of movement at individual-level and the diffusion equation as a description of dispersal at population-level [29], [107].

Random Walk Process

Consider an individual moving on a one-dimensional uniform lattice (i.e. a spatial domain x divided into finite sites of length Δx). At each time step Δt, this individual

can move a short distance Δx, to the left or to the right with probabilities l and r, respectively, or stays in the same location ('waits'), with probability $1 - l - r$.

If the individual is at location x at time $t+\Delta t$, then there are three possible locations this individual can occupy at time t [29], [194]:

I this individual was at $x + \Delta x$ and it moved left (with probability l).

II it was at $x - \Delta x$ and then moved to the right (with probability r).

III it was at x and did not move at all (with probability $1 - l - r$).

Let us define the term $p(x, t)$ as the probability density function for the location of the individual after time t. Thus, the master equation that can relate probabilities at different time steps is given by:

$$p(x, t + \Delta t) = p(x + \Delta x, t)l + p(x - \Delta x, t)r + p(x, t)(1 - l - r) \tag{2.27}$$

Assuming Δx and Δt are small, equation (2.27) can be expanded in Taylor series, which gives:

$$\begin{aligned}
&p(x,t) + \Delta t \frac{\partial p}{\partial t}(x,t) \\
&= l\left\{p(x,t) + \Delta x \frac{\partial p}{\partial x}(x,t) + \frac{\Delta x^2}{2}\frac{\partial^2 p}{\partial x^2}(x,t)\right\} \\
&+ r\left\{p(x,t) - \Delta x \frac{\partial p}{\partial x}(x,t) + \frac{(\Delta x)^2}{2}\frac{\partial^2 p}{\partial x^2}(x,t)\right\} + (1-l-r)p(x,t) + o(\Delta t^2, (\Delta x)^2)
\end{aligned}$$

Setting $\epsilon = r - l$ and $\varphi = r + l$:

$$\begin{aligned}
&p(x,t) + \Delta t \frac{\partial p}{\partial t}(x,t) \\
&= \varphi p(x,t) - \Delta x \epsilon \frac{\partial p}{\partial x}(x,t) + \varphi \frac{(\Delta x)^2}{2}\frac{\partial^2 p}{\partial x^2}(x,t) + (1-\varphi)p(x,t) + o(\Delta t^2, (\Delta x)^2)
\end{aligned}$$

This equation can be simplified to yield:

$$\frac{\partial p}{\partial t} = -\frac{\Delta x \epsilon}{\Delta t}\frac{\partial p}{\partial x} + \frac{\varphi(\Delta x)^2}{2\Delta t}\frac{\partial^2 p}{\partial x^2} \tag{2.28}$$

We assume that the movement is unbiased, meaning that there is no preferred direction (the walk is completely random). Following this assumption, we can set $r = l = v$ ($\varphi = 2v$ and $\epsilon = 0$). Taking the limit $\Delta x, \Delta t \to 0$ with $\frac{(\Delta x)^2}{\Delta t}$ remains positive and constant yields diffusion equation:

$$\frac{\partial p}{\partial t} = D\frac{\partial^2 p}{\partial x^2} \tag{2.29}$$

where D is known as diffusion coefficient, such that:

$$D = \frac{v(\Delta x)^2}{\Delta t} \tag{2.30}$$

with v as the probability of moving to the left or right. The solution to (2.29), corresponding to the point release of a species, is a Normal centred about zero [29], [194]:

$$p(x,t) = \frac{1}{\sqrt{4\pi Dt}} exp\left(\frac{-x^2}{4Dt}\right) \tag{2.31}$$

As an example, Figure 2.6 shows five realisations of random walk with 100 steps. These realisations correspond to the possible paths of an individual can move in 100 time steps, starting from the origin. We can see the random nature of the movements and also the increasing distance from the origin as time progresses [107].

A Diffusion Model

In the previous section, we demonstrate that the random walk process can be used to derive the diffusion equation. In general, the diffusion model is given by the following equation:

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} \tag{2.32}$$

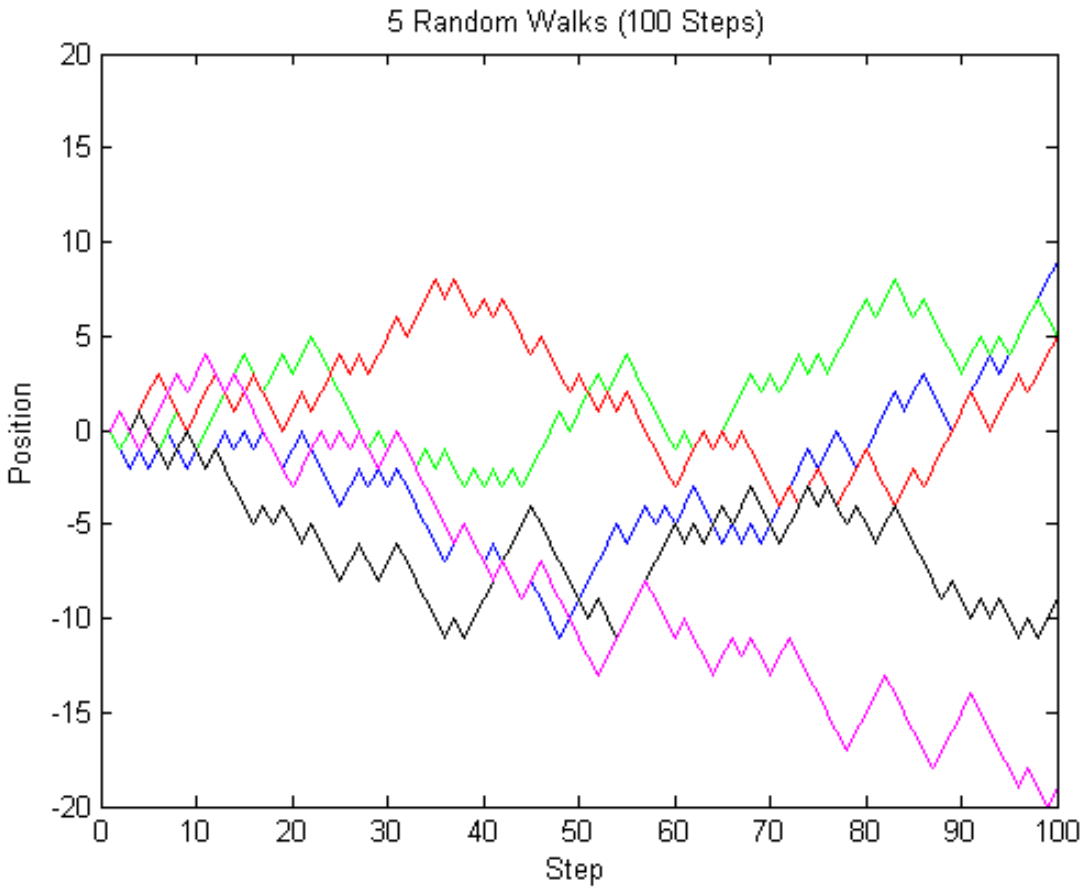


FIGURE 2.6: Five realisations of a random walk along one-dimensional lattice with step length of 1 (after 100 time steps). The probabilities of moving left and right: $l = r = 0.5$.

where N is the density of species and D is the diffusion coefficient. The diffusion model (2.32) assumes that the dispersal pattern of species is localised (meaning that species are assumed to disperse between adjacent spatial locations). This assumption is consistent with the spatial dispersal distributions of some species; for instance, some plant seeds are often dispersed over short distances and near to their parents' locations [20], [147].

Simulating equation (2.32), we observe (Figure 2.7) a dispersal behaviour which is directed from highly populated locations to less populated locations as time increases, with D describes the strength of dispersal at which the population moves down these gradients. In general, the higher D the faster the dispersal process occurs. For further details and extensions of the concepts on the local dispersal process, the reader is referred to [93], [145].

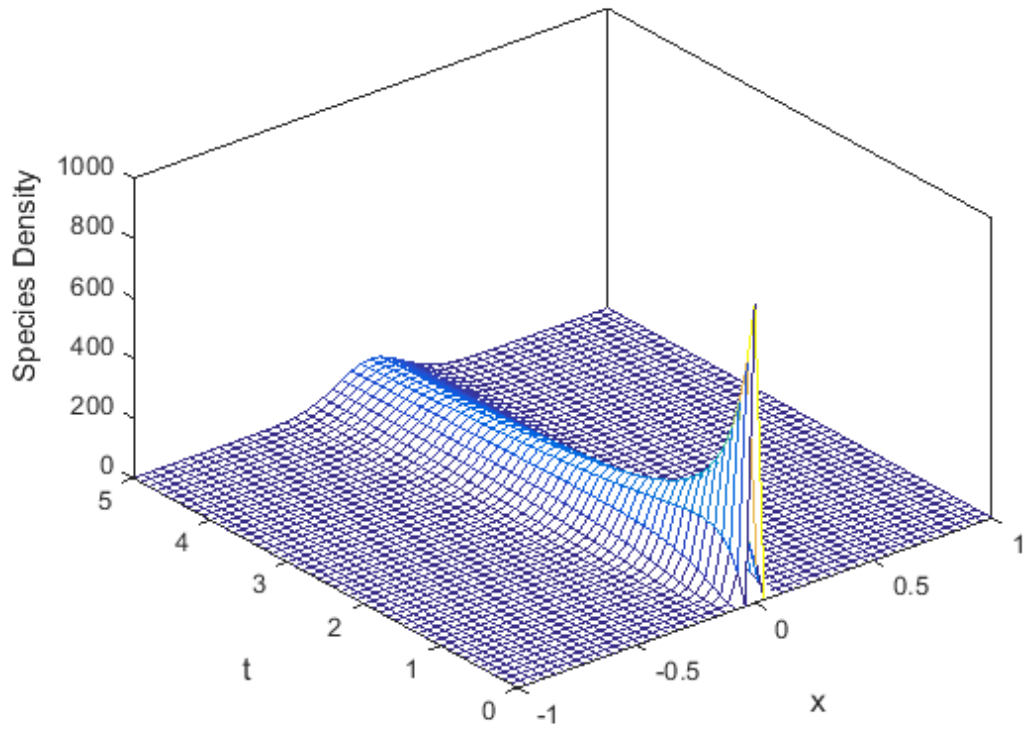


FIGURE 2.7: Dispersal pattern of the population based on the diffusion model (2.32) with $D = 0.002$. Population initially starts at $t = 0$ and located at $x = 0$. Equation (2.32) is solved numerically with the method of lines using MATLAB `pdepe` solver (as described in Section 4.2.1).

Applications of Local Dispersal Models

In practice, diffusion equations have been used to model movement of species in mark-recapture studies e.g. flea beetle species [111]. Empirical studies have also demonstrated that the predictions of this equation match the observed spread of some species such as white cabbage butterfly and grey squirrels [76]. This equation has also been incorporated into several single-species deterministic growth models (as discussed in Section 2.2.2) to examine how the density of population changes as a result of dispersal-growth process [53], [172]. For instance, inclusion of a diffusion term into a logistic growth model will result in a Fisher's equation [53]; this equation is used in various fields such as ecology, cell biology and population genetics to study the range expansion and the spread of single-species population [168]. In an early work, Skellam [172]

studied the range expansion of muskrat populations using a diffusion model with exponential growth process; he discovered that the area occupied by the muskrat populations increases linearly with time.

2.4.2 Non-Local Dispersal Process

A Dispersal Kernel Formulation

While the diffusion equation has been used successfully to predict the spread of some focal species, such as muskrats and butterflies, it has also been demonstrated that this model underestimates the rate of spread of other species, like beetles [10]. In the case of beetle species, Andow et al. [10] find that the diffusion model performs poorly because it does not incorporate non-local dispersal effects. In nature, the dispersal process of some species can occur over non-adjacent spatial locations and larger distances [107], [147]. For instance, some plants can disperse their seeds over larger distances by using a variety of dispersal vectors, including animals, wind and water [20], [43], [95], [98], [147].

To examine the effects of non-local dispersal across locations on the dynamics of populations, we consider an integro-differential equation (IDE), which takes the form:

$$\frac{\partial N}{\partial t} = \rho \left[\int k(x-y)N(y)dy - N(x) \right] \tag{2.33}$$

where N is the density of species, $k(x-y)$ is the probability density function of species moving from location y to x (i.e. dispersal kernel) and ρ is the the dispersal rate of non-local dispersal process. Generally, dispersal kernels with fat-tailed shape (meaning a higher probability of long-distance dispersal than a normal distribution) and higher central peak are often used in modelling non-local dispersal patterns [107]; however, the fat-tailed dispersal kernels may have some moments infinite [127]. For further details and extensions of the concepts on the non-local dispersal process, the reader is referred to [89], [101], [117], [127], and also our work in Chapter 6.

Applications of Non-Local Dispersal Models

Non-local dispersal models have been validated in numerous ecological studies. For instance, non-local dispersal kernels has been shown to fit the spatial distribution of *Drosophila* species [117]. Dispersal kernel formulation has also been used to model the non-local dispersal process of pied flycatcher species [25]. Additionally, empirical studies of plant populations have shown that a non-local dispersal model provides a better fit for the dispersal process of spores and pollen [73].

2.5 Modelling Background of the Study

Predicting which species will be present (or absent) across a geographical region, remains one of the important issues in ecology [61], [167], [199]. Predictions of presence-absence often focus on the influence of environmental variables such as climate on species [112], [157], [173], yet other factors such as biotic interactions, dispersal and demographic stochasticity can also affect community dynamics and their range limits [60], [95]. These ecological processes have been incorporated into different modelling frameworks to investigate the dynamics of ecological systems [23], [62], [95], [109]. In general, the ecological processes such as dispersal and growth can be described at different perspective, either population level or individual level [5], [41], [149], [161], [198]. In the former case, the dynamics of species are modelled using deterministic systems (as discussed in Section 2.2.2 and 2.3.1) in which the population of species are represented in terms of continuous densities. In the latter case, the stochastic individual-based models (IBM) can be used in which the interacting species are represented as sets of discrete individuals and stochastic events such as birth and death (as discussed in Section 2.2.1) are often considered in modelling their presence-absence. Here, we investigate the combined influences of several ecological forces, namely biotic interactions, abiotic environments and dispersal process on multi-species community dynamics using deterministic and stochastic models.

Deterministic Models with Biotic Interactions

Deterministic models have long been employed in ecology, with the goal is to understand how the size of population changes as a result of the growth [129], [192], [193] and also dispersal [53], [172] processes. As discussed in the previous section, some of the well-known deterministic population dynamics models are single-species logistic equation [192] and two-species Lotka-Volterra models [129], [193]. Such models generally take the form of differential equations, in which they aim to understand the interactions between species at the population-level [23], [94], [95], [120], [198]. In general, the deterministic models follow a mean-field assumption, which assumes that individuals interact in proportion to their average density and ignores the presence of any small-scale behaviour [44]. This modelling framework has been used to investigate the roles of biotic and abiotic factors in determining the presence-absence of species. By employing deterministic Lotka-Volterra models [129], [193], Roughgarden [164] and MacLean and Holt [133] analyse the range limits of two competing species along environmental gradient. They discover that competitive interactions can determine range limits when these species vary inversely over locations [164], or when species respond similarly to environmental gradients [133]. By incorporating a third species into Lotka-Volterra competition models [129], [193] with environmental gradients, Holt and Barfield [94] illustrate that this inclusion can modify the range limits of two competing species. Godsoe et al.[69], [70] extend previous deterministic two-species models [23], [133], [164] along environmental gradients and identify situations where small changes in two-species interactions result in large shifts in range limits. In this situation, their analysis reveals that accurate knowledge of species' environmental tolerance and biotic interactions are crucial in order to predict species presence-absence [69], [70]. One significant limitation to these previous investigations is that they often focus on the dynamics of two interacting species. In reality, ecological systems are complex and may involve more than two species. It is important to consider a system of more than two species, in order to better understand the possible influences species can have on one another in a multispecies community [94], [156]. Thus, in Chapter 3, we provide further research in this direction by extending a simple Lotka-Volterra competition system to model biotic interactions among multiple species across heterogeneous environments [133],

[164], and investigating the resulting dynamics of the system.

Local Dispersal Models with Biotic Interactions

Numerous studies show that dispersal can affect the dynamics of population [11], [13], [21], [23], [124]. As illustrated in Section 2.4.1, one of the ways to model dispersal process is to use a deterministic diffusion equation. In the diffusion model, species are assumed to disperse between neighbouring locations following a local dispersal process [29], [194]. The diffusion equation can be incorporated into deterministic models with biotic interactions to explore the interplay of local dispersal and species interactions in determining the dynamics of ecological systems. This inclusion leads to a system of partial-differential equations (PDE), which is one of the famous approaches in ecological modelling [1], [22], [93]. This modelling framework has been employed in order to gain insight into various fundamental population processes, such as, the combined influences of biotic interactions and dispersal, habitat geometry and edge effects and dispersal-mediated coexistence phenomenon [93]. For instance, Alzahrani et al. [8] employ Lotka-Volterra competition model with local dispersal and discover that the competitive outcomes depend both on the strength of biotic interaction and the diffusion coefficients. By using similar modelling framework, Cantrell and Cosner [21] show that local dispersal of species can reduce the detrimental effect of competition and promote species coexistence. Other modelling studies [151] also show that several ecological processes, such as environmental response, biotic interactions and local dispersal, can determine species presence-absence across a geographical region. Case et al. [23] examine two-species competition models with local dispersal. They demonstrate that abrupt range limits may arise due to biotic interactions in either homogeneous [23], [126] or heterogeneous environments [23]. It has also been shown that when biotic interactions are relatively weak, coexistence of species is possible; when biotic interactions are strong, priority effects occur with species presence-absence depends on initial abundances and dispersal intensity [23]. While most of these previous studies have investigated the roles of biotic interactions and dispersal in determining species presence-absence, there have been less attention paid to the combined influences of priority effects and dispersal in shaping multi-species community dynamics.

As discussed in Chapter 1, the establishment order of species can greatly affect community dynamics, and cause local community to exhibit alternative community compositions. However, much less is known about what effect local dispersal can have on the occurrence of priority effects in multi-species communities once biotic interactions and abiotic environments are present. In Chapter 4 and Chapter 5, we provide some insights into the conditions under which priority effects occur and disappear as dispersal intensity changes.

Stochastic Individual-Based Models

To investigate how the underlying population-level information relates to a smaller individual scale, we also develop a stochastic model, which is constructed to be comparable with the deterministic model. In particular, we employ stochastic individual-based models (IBM) whereby the interacting species are represented as collections of discrete individual agents; these agents are tracked explicitly over time while undergoing birth-death process or dispersing over adjacent locations [120], [149], [161], [197], [198]. To do this, we use random walk theory and stochastic birth-death process, as discussed in Section 2.4.1 and Section 2.2.1, respectively. In general, different studies [120], [198] have illustrated agreement and/or disagreement between predictions of stochastic and deterministic models. For instance, Faugeras and Maury [50] develop a random walk model to study the movements of fish population and derived a deterministic model which approximates their stochastic IBM; they discover that the deterministic results appear to follow closely the results of the stochastic IBM. Allen and Allen [6] investigate several single-species stochastic models, which correspond to the deterministic logistic model; they illustrate that the stochastic predictions can vary for different populations that experience the same logistic growth. Law et al. [120] investigate a single-species IBM and show that the IBM predictions can be different compared to the logistic equation. Wilson [198] develops IBM with biotic interactions and dispersal process; he demonstrates qualitative agreement between the IBM and deterministic results. By reducing the total population size, he also illustrates the disagreement between the IBM and deterministic predictions [198]. Additionally, IBMs have been used to understand the possible outcomes of species interactions in ecological communities

[59], [182], [195]. For instance, Weisberg and Reisman [195] examine the stochastic IBM with prey-predator interactions and show that the IBM can exhibit several possible dynamics including oscillatory behaviour. Tam and Ang [182] study an IBM of a coral reef community and find that priority effects can occur as a result of competitive biotic interactions. It is also interesting to note that these modelling approaches are used in other fields such as epidemiology [3], [4], microbiology [51], [52], [59], [119], animal behaviour and species movement [68]. Some of these studies [3], [4], [52], [59] propose the use of stochastic models to predict the dynamics of interacting individuals in the case of small populations. This is because stochastic variation can cause species with small populations to become absent at certain sites [59]. With respect to the aforementioned studies, it remains unclear about the effect of population size on the occurrence of priority effects in the stochastic systems. At present, it is still not known whether the combined influences of dispersal and stochasticity can lead to appearance or disappearance of priority effects when the size of population varies between large and small populations. Based on this information, in Chapter 5, we employ a stochastic IBM to investigate the interaction of priority effects with local dispersal and stochasticity in shaping species presence-absence for different population sizes.

Non-Local Dispersal Models

As discussed in Section 2.4.2, a non-local dispersal process can also affect the dynamics of natural communities [20], [147]. For example, while it is found that squirrels can disperse acorns over short distances, other dispersal vectors such as blue jays can transport acorns over larger spatial ranges [43], [95]. This example illustrates that long-distance dispersal events are also important particularly when considering the case of certain species that can disperse their offsprings larger distances. It has been proposed that long-distance dispersal events need to be incorporated into modelling frameworks if we want to improve our predictions on species presence-absence [88]. Inspired by this empirical evidence, we also examine the impacts of different dispersal patterns on community dynamics. For such situations, some non-local dispersal models have been formulated [85], [101], [109], which often take the form of integro-differential equations (IDE). For instance, Hetzer et al. [85] study a two-species Lotka-Volterra competition

model with long-distance dispersal; they discover that non-local dispersal process can affect community dynamics with faster disperser can lead to extinction. Kao et al. [108] show that when different species employ different dispersal patterns, the presence-absence of species depends on dispersal intensity with slower disperser can survive and exclude the other species. In another study, Kao et al. [109] also demonstrate the significance influences of both local and non-local dispersal mechanisms in determining species presence-absence. Hutson et al. [101] find that the non-local dispersal process can affect species presence-absence, and the dynamics of species interactions can vary with dispersal distance and its magnitude. A consistent observation in these studies is that dispersal distance has an effect on the dynamics of interacting species. However, these results are based upon two-species system and it is unclear what effect non-local dispersal will have on multi-species community assembly under varying dispersal strength and in the presence of priority effects. By employing different dispersal models, in Chapter 6, we explore the effects of non-local dispersal process on the occurrence of priority effects in comparison to a local dispersal process. Additionally, we also examine the consequences of different modes of dispersal on species coexistence in multi-species communities.

Two-Dimensional Space Models

The final part of this thesis is to develop a two-dimensional (2-D) space PDE model. In this case, species environmental suitability may depend on two variables, rather than one. Our aim is to investigate whether the 1-D and the 2-D space models yield qualitatively similar dynamics. As discussed earlier, the PDE models have been employed to examine the spatial dispersal and growth process of different species since in early work of [53], [172]. For instance, Okubo et al. [150], [168] use the 2-D PDE models to explore the growth and local dispersal processes of two squirrel species in Britian; they found that the invasive grey squirrels can establish themselves and displace the native red squirrels. This modelling framework is also employed to examine the effects of local dispersal in promoting coexistence of strongly competing species [93], [126], [139]: in the absence of dispersal, priority effects occur with only one species can survive

[126]; inclusion of dispersal can allow coexistence of species [139]. Comparative studies between the 1-D and 2-D space models have also identified the mechanisms that can facilitate species coexistence [135], [144], [197]; in particular, Morozov and Li [144] show that coexistence of species is more pronounced in a 2-D space model, in comparison to a 1-D space model; they characterise this phenomenon as space-mediated population persistence. Other studies [135], [197] also demonstrate that increasing the spatial dimension of ecological systems can influence the mechanisms of species persistence and coexistence. Motivated by these observations, we compare the predictions of the 1-D space model with the 2-D space models in Chapter 7. Our aim is to develop an understanding of when the predictions of priority effects and species coexistence are similar in these two models.

Chapter 3

Biotic Interactions and Abiotic Environments

3.1 Introduction

The previous chapter provides review on the deterministic model of biotic interactions and their dynamical behaviours. This non-spatial model assumes that species interactions occur in a well-mixed environment, and describes the presence-absence of species as spatially homogeneous (i.e. constant distributions throughout space). In reality, the presence-absence of species are rarely, if ever, constant throughout spatial locations. Environmental factors such as climate can affect the presence-absence of species across a geographical region [78], [112], [169], [173], [196]. It has been demonstrated through empirical evidence that environmental factors can determine species range limits in marine and terrestrial communities [158], [174]. For instance, Barry et al. [12] discover that changes in shore temperature can affect species presence-absence in intertidal communities; Perry et al. [158] demonstrate that the distributions of fish species have shifted in mean latitude (or depth) because of increases in sea temperature; Comte and Grenouillet [32] suggest that climate can affect the distributions of stream fish species along environmental gradients; Moritz et al. [143] illustrate that the distributions of some small mammals have changed due to the influence of climate.

Apart from environmental components, biotic interactions has also been proposed as another crucial factor that can shape species range limits [23], [67], [69], [199]. The notion that biotic interactions such as competition can influence the presence-absence

of species dates back to early work by Darwin [36]. In general, the effect of biotic interactions in determining community dynamics has received great attention in ecology; this is due to the influential role that competitive interactions play in the development of ecological theory; from the concept of niche by Grinnell [75], to Lotka [129] and Volterra's [193] models and Gause's [64] work on the competitive exclusion principle, to Hutchinson's work [100] on the concept of fundamental and realized niches. This idea is also supported by an early experimental study that is discussed in Chapter 1: for instance, Connell [34] illustrated that the presence-absence of barnacles were determined by desiccation and biotic interactions with other species [34].

Experimental work of Connell [34] also illustrates that the combined effects of biotic interactions and abiotic environments can shape community dynamics across heterogeneous environments [140]. It has been observed in different studies that both biotic and abiotic components can influence community compositions; for example, by studying the competition between exotic and native Daphnia species, Wittmann et al. [200] illustrate that the outcomes of species interactions depends on temperature and competitive interactions. The work of Johnson and Havel [104] also confirms the significant roles of both biotic and abiotic factors in shaping species presence-absence. Experimental evidence by Harley [83] demonstrates that environmental factors such as climate can affect biotic interactions among species and determine community assembly. Through warming experiments, Suttle et al. [179] illustrate how the interplay of biotic interactions and climate can shape species presence-absence in grassland communities.

Overall, the aforementioned studies show that the interplay between biotic interactions and abiotic environments can significantly determine community assembly. Motivated by these observations, we aim to investigate the joint influences of biotic interactions and environmental factors in determining species range limits. To do this, we extend previous deterministic theoretical studies involving two interacting species [133], [164] to model biotic interactions among multiple species across heterogeneous environments. The method is a spatially explicit extension of the Lotka-Volterra competition model [23], [69], [164], which will be discussed in the next section. The remainder of the chapter is organized as follows. After describing this deterministic model, we derive several analytical results on range limits of species. Based on these

analytical expressions, we discuss some biological mechanisms that can significantly shift the range limits in multi-species communities. Additionally, numerical results are presented, and comparisons of analytical with numerical results on the range-limit predictions have indicated agreement between the two results. By using this model, we also examine the possible outcomes of species interactions such as coexistence of species and priority effects, as the strength of biotic interactions changes. In the presence of priority effects, competitive exclusion of all but one species occurs; in this case, initial species abundance is a critical feature in determining the range limits of strongly interacting species. Ecologically, this critical feature could be utilised as a biocontrol strategy: by manipulating the initial abundances of the interacting species appropriately, in particular the initial abundances of the biocontrol agents.

3.2 A Deterministic Model with Biotic Interactions and Environmental Suitability

We employ a multi-species deterministic model by extending the Lotka-Volterra competition equations along environmental gradients [23], [70], [164]. Specifically, we consider a system of ordinary-differential equations (ODE) for the densities N_i of m species:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = \frac{r_i N_i}{K_i}\left(K_i - \sum_{j=1}^{m} \alpha_{ij} N_j\right) \qquad (i = 1, 2, ..., m) \tag{3.1}$$

where r_i is the intrinsic growth rate of species i, K_i is the carrying capacity and α_{ij} is the competitive effect of species j on species i. By rescaling the density of species i relative to its intraspecific competition coefficient α_{ii}, we may effectively set the intraspecific competition coefficients α_{ii} to equal 1, and the remaining competition coefficients α_{ij} represent the ratio of intraspecific to interspecific competition. The suitability of a particular environment or location is modelled by incorporating a spatial dependence x into the carrying capacity term; each species' carrying capacity $K_i(x)$ can vary with location x. x could be a location within a geographical region, or used as a proxy for representing abiotic environmental factors such as temperature, moisture or elevation

that affect the carrying capacity of species. The effects of biotic interactions on range limits can depend on how each species responds to the environmental gradient. To illustrate these effects in a multispecies community, we use a linear environmental gradient (i.e. carrying capacity varies linearly with x) [23], [70], [164]:

$$K_i(x) = m_i x + c_i \tag{3.2}$$

where $K_i(x)$ is carrying capacity of species i at location x, m_i is the change in environmental suitability with respect to abiotic component x and c_i is the carrying capacity of species i when $x = 0$.

The dynamical behaviour of equation (3.1) at a specific location x is independent of the behaviour at all other locations. Competition is assumed to be local, meaning that species only compete with other species at the same location. In general, the simplest equation of type (3.1) is in the case of two-species (i.e. $m = 2$). As discussed in Section 2.3.1, competitive interactions within each location x lead to several outcomes, depending on the competition coefficient and the ratio of the carrying capacities $\frac{K_1}{K_2}$: stable coexistence (when $\alpha_{12} < \frac{K_1}{K_2} < \frac{1}{\alpha_{21}}$) and priority effects (when $\frac{1}{\alpha_{21}} < \frac{K_1}{K_2} < \alpha_{12}$). The analysis can be extended for the case more than two interacting species (i.e. $m = 3$); the reader is referred to [24], [27], [72], [118] for further details and extensions of these dynamical systems results.

3.2.1 Numerical Methods

In the next section, we derive several analytical results on range limits of species using MAPLE. We also present some numerical simulation results to illustrate the possible outcomes of the model (3.1). For numerical results, equation (3.1) is solved numerically using Runge-Kutta method with MATLAB `ode45` solver for $t = 1000$. We used initial conditions as indicated in each figure section. To verify that the steady state is stable (i.e. all the real parts of the eigenvalues are negative), equation (3.1) is analysed using MAPLE `linalg` package by seeking steady states and performing a stability analysis, as discussed in Section 2.3.1.

TABLE 3.1: Parameter values for the left and right columns of Figure 3.1 and Figure 3.3.

Symbol	Description	Parameter Value	
		Left Column	Right Column
r_i	The intrinsic growth rate of species i	1	1
m_1	Steepness of the K_1-gradient	1	1
m_2	Steepness of the K_2-gradient	0	0
m_3	Steepness of the K_3-gradient	0.9	2
c_1	Carrying capacity of species 1 when $x = 0$	0	0
c_2	Carrying capacity of species 2 when $x = 0$	0.4	0.4
c_3	Carrying capacity of species 3 when $x = 0$	0	-0.8
α	Competition coefficient (values given in figure captions)		

We also employed numerical continuation package XPPAUT to check our simulation results. Equation (3.1) is solved for steady state using `cvode` solver for $t = 1000$. Then, the steady state is continued in AUTO, in which we tracked stable and unstable steady states and also bifurcation points as a model parameter changes. Continuation results shown in this chapter used a maximum/minimum allowable step size of parameter, $10^{-1}/10^{-6}$. Unless otherwise stated, parameter values used in the simulation are given in Table (3.1).

3.3 Analytical Results on the Range Limits of Species

We first discuss some of the analytical results in the two-species model ((3.1) with $m = 2$). We assume throughout this analysis that x increases from 0 to 1. Godsoe et al. [70] present results on the two competing species case. They analyse the range limits of species (i.e. species 1 and 2) using the idea of invasion points, x_i (i.e. the boundaries of the locations at which a species i can invade when rare). The invasion points divide the location into several regions: one where species 1 (respectively, species 2) are present and species 2 (respectively, species 1) are absent, and a central region where the possible dynamics depend on the strength of biotic interactions, α. We can calculate the invasion points x_i explicitly and discuss the biological mechanisms that influence the range limits of species. In general, species i can invade when rare if the growth rate of this species is positive [84]. In the Lotka-Volterra model (3.1) with $m = 2$, this condition corresponds to setting the right-hand side of equations (3.1) to be larger than zero and taking $N_i(x) \approx 0$ and $N_j(x) \approx K_j(x)$. This gives us $K_i(x) > \alpha_{ij} K_j(x)$. The point x

satisfying:

$$K_i(x) = \alpha_{ij} K_j(x) \tag{3.3}$$

corresponds to the invasion point of species i. Based on linear carrying capacity as given by equation (3.2), Godsoe et al. [70] analyse the situation when the carrying capacity of species 1 (focal species) is 0 at $x = 0$ (i.e. by setting $c_1 = 0$). The invasion point of species 1 is given by:

$$x_1 = \frac{\alpha_{12} c_2}{m_1 - \alpha_{12} m_2} \tag{3.4}$$

They discuss two biological mechanisms that cause a change in x_1 (given by equation (3.4)) and thus shift the range limit of species 1 [70]:

Mechanism A When there is a rapid change in competitive outcome along environmental gradient. This occurs when species 2 exerts strong interspecific competition near the boundary of fundamental niche of species 1 (i.e. $\alpha_{12} c_2$ is large)

Mechanism B When there is a slow change in competitive outcome along environmental gradient, meaning that the change in the carrying capacity of species 1 (K_1) is similar to the change in the effect of competition from species 2 ($\alpha_{12} K_2$) along the environmental gradient. As the denominator of equation (3.4) becomes very small ($m_1 - \alpha_{12} m_2 \to 0$), the invasion point of species 1 shifts rapidly with additional changes in K_i

For mechanism A, this case corresponds to the competition between two ecologically different species (i.e. their carrying capacities vary inversely over x); when mechanism A dominates, small changes in model parameters produce small changes in the range limit of species 1 [70]. For mechanism B, this situation corresponds to the interaction between two ecologically similar competitors (i.e. their carrying capacities vary similarly over x); when mechanism B shapes the range limit, small changes in model parameters can cause a large change in x_1 [70].

In reality, ecological systems are often complex and involve more than two species.

It is important to consider a system of more than two species, in order to better understand the possible influences species can have on one another in a multispecies community [156]. To begin with, we study the range limits of three interacting species ($m = 3$) in the model (3.1) when there is an interplay between the rapid and slow changes in competitive outcomes along environmental gradients, which may provide an example of complex multi-species interactions. To do this, we study a special case consisting of two ecologically similar species (e.g. species 1 and 3) and one ecologically different species (e.g. species 2), with the environmental gradients and the strength of interspecific competition are given by:

1. The coordinate $x = 0$ indicates the point at which the carrying capacities of species 1 equal 0 and K_1 increases with x (i.e. setting $m_1 > 0$ and $c_1 = 0$).
2. Species 2 is homogeneously distributed across x (i.e. setting $m_2 = 0$).
3. Carrying capacity of species 3 increases with x (i.e. setting $m_3 > 0$ and $c_3 \leq 0$).
4. These species have the same strength of biotic interactions (i.e. setting $\alpha_{ij} = \alpha$).

We concentrate our analysis on two focal species, hereafter labelled species 1 and 3. The possible dynamics can be explained by keeping track of which species can invade when rare and the number of competing species present. If there is only one competitor present (e.g. species 2) and either species 1 or species 3 can invade when rare (depending on the magnitude of K_1 and K_3), then this is analogous to the two species case discussed by Godsoe et al. [70]. Without loss of generality, we could assume that species 1 has a sufficiently higher carrying capacity than species 3 in some portion of location x. In the presence of species 2, species 1 can invade when rare if $K_1(x) > \alpha_{12} K_2(x)$. The invasion point can still be defined by equation (3.4) whereby x_1 will satisfy:

$$x_1 = \frac{\alpha c_2}{m_1} \tag{3.5}$$

To the right of x_1, we have two species present (e.g. species 1 and 2). In this situation, species 3 can invade when rare if the growth rate of species 3 is positive [84]. This condition corresponds to setting the right-hand side of equations (3.1) to be larger than

zero and substituting $N_1 = N_1^*$ and $N_2 = N_2^*$, which correspond to the steady states of species 1 and species 2, in the absence of species 3 ($N_3 = 0$). Thus, species 3 can invade when rare if $K_3(x) > \alpha N_1^* + \alpha N_2^*$. The invasion point x_3 will satisfy:

$$K_3(x) = \alpha(N_1^* + N_2^*) \tag{3.6}$$

with N_1^* and N_2^* are given by (computed using MAPLE):

$$N_1^* = \frac{m_1 x - \alpha c_2}{1 - \alpha^2} \text{ and } N_2^* = \frac{c_2 - \alpha m_1 x}{1 - \alpha^2} \tag{3.7}$$

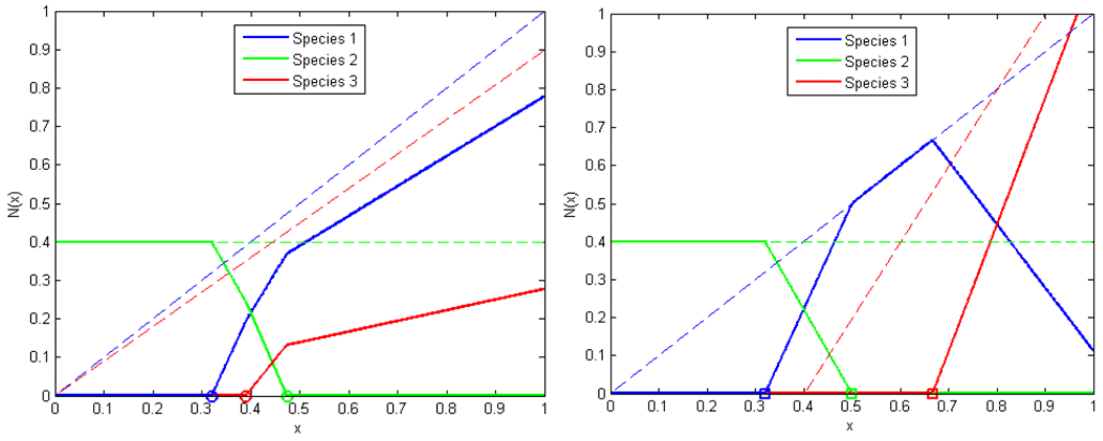
Substituting the expressions for N_1^* and N_2^* in (3.7) into (3.6) with $K_3(x) = m_3 x$, we can solve for x (computed using MAPLE):

$$x_3 = \frac{\alpha c_2}{(1+\alpha)m_3 - \alpha m_1} \tag{3.8}$$

Based on equation (3.8), the mechanisms by which biotic interactions influence x_3 are analogous to the two competing species case. Notice that when αc_2 gets larger, this can increase x_3 and shift the range limits of species 3 away from its fundamental niche. This is analogous to mechanism A i.e. rapid changes of competitive outcomes along environmental gradients. Ecologically, when mechanism A dominates, modest changes in the biology of competitors can produce modest changes in the range limit of species 3.

The invasion point of species 3 also increases when the change in the combined effect of species 2 and 3 ($(1+\alpha)m_3$) is similar to the change in the effect of species 1 along the environmental gradient (αm_1), which is analogous to mechanism B, slow change in competitive outcomes. Mathematically, there is an asymptote ($x_3 \to \infty$) when $(1+\alpha)m_3 - \alpha m_1$ tends to 0. When mechanism B dominates, small changes in the biology of competing species can cause large changes in the range limit of species 3. Similarly, in the presence of species 1 and 3, we can identify the invasion point of species 2:

$$x_2 = \frac{(1+\alpha)c_2}{\alpha(m_3 + m_1)} \tag{3.9}$$



(A) $K_3(x) = 0.9x$ (B) $K_3(x) = 2x - 0.8$

FIGURE 3.1: The steady-state of the model (3.1) with $m = 3$ and $\alpha = 0.8$ following linear environmental gradient (3.2). Carrying capacity of species 3: (A) $K_3(x) = 0.9x$ to (B) $K_3(x) = 2x - 0.8$. Solid lines indicate steady-state of $N_i(x)$; dotted lines indicate carrying capacity $K_i(x) = m_i x + c_i$; circles and squares show the locations of the invasion points x_i (with equations (3.5), (3.8) and (3.9) represent the invasion points of species, x_1 , x_3 and x_2, respectively for (A); and equation (3.3) can be used to determine x_i for (B)). Initial abundances: $N_1(x) = 0.9K_1(x)$, $N_2(x) = 0.1K_2(x)$, $N_3(x) = 0.1K_3(x)$. Other parameter values as in Table (3.1). This result is computed using MATLAB `ode45` solver.

3.4 Results: The Effects of Biotic Interactions on the Presence-Absence of Species

In this section, we present the numerical results of the model (3.1). Overall, comparisons of analytical with numerical results on the range-limit predictions have indicated agreement between the two results. We also discuss the influence of biotic interactions on species presence-absence: when biotic interactions are relatively weak ($\alpha < 1$), coexistence of species is possible; however, when biotic interactions are relatively intense ($\alpha > 1$), this situation leads to priority effects; consequently, the presence-absence of species depends on initial abundances of species.

3.4.1 Species Presence-Absence When $\alpha < 1$: Coexistence of Species

As an example, Figure 3.1 shows the range limits of species predicted by the model (3.1) when $\alpha < 1$. In particular, Figure 3.1A and Figure 3.1B illustrate the possible dynamics when $\alpha = 0.8$, with two different environmental gradients (dotted lines) for species 3 (red) e.g. $K_3(x) = 0.9x$ and $K_3(x) = 2x - 0.8$, respectively (other parameter

values remain the same as in Table (3.1)). We observe that when biotic interactions are relatively weak ($\alpha < 1$), then coexistence of species is possible.

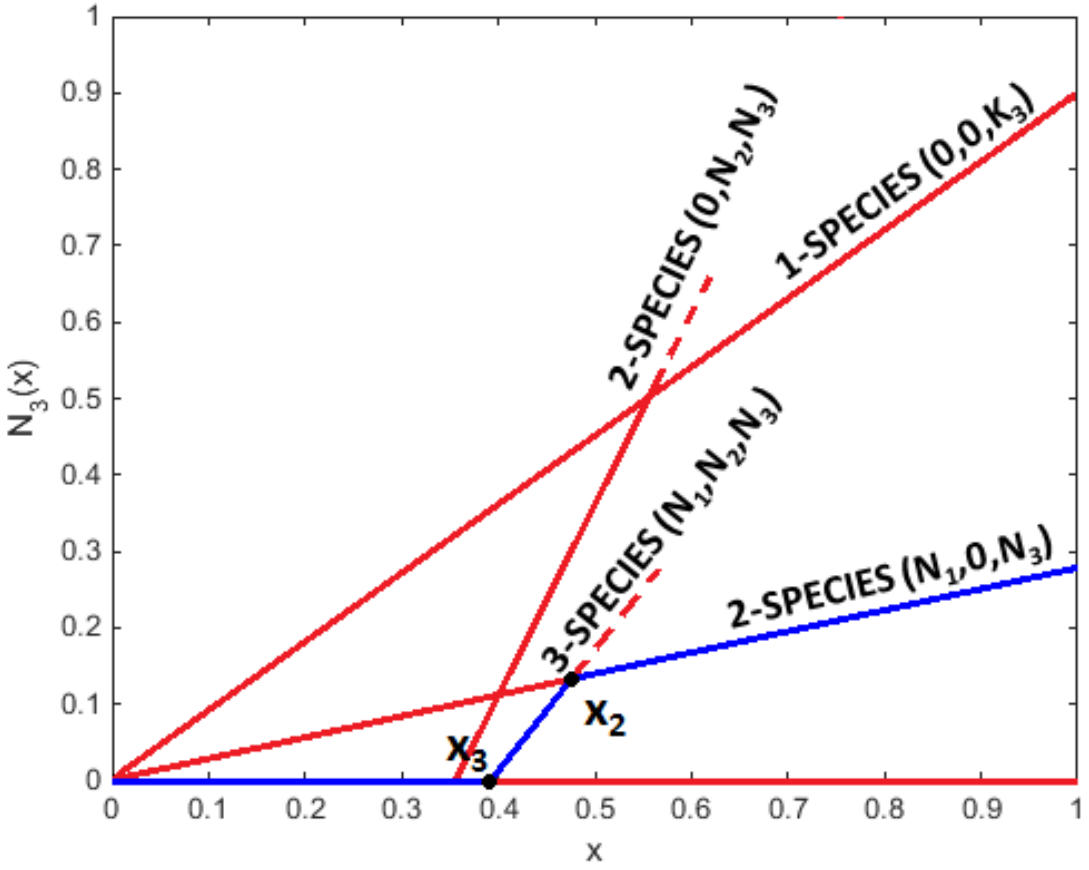


FIGURE 3.2: The density of a focal species (species 3) when $\alpha = 0.8$ for the model (3.1) with $m = 3$ as x changes. Linear environmental gradient (3.2) with carrying capacity of species 3, $K_3(x) = 0.9x$ (as in Figure 3.1A). The threshold values x_i correspond to transcritical bifurcation points (black points). Blue and red curves indicate stable and unstable steady-states as described in the figure. Solid and dotted curves indicate ecologically feasible solution and infeasible solution (i.e. one of the densities of species is negative). Other parameter values as in Table (3.1). This plot is computed by numerical continuation using XPPAUT.

Based on Figure 3.1A, competition from species 2 (green) eliminates species 1 (blue) from some locations x and shift the range limit of species 1 from $x = 0$ to $x = 0.32$ (blue circles); similarly, the range limits of species 2 (green circles) and species 3 (red circles) are affected due to biotic interactions from their competitors. The range limits of species 1, 2 and 3 can be represented using invasion points x_i, described by equations (3.5), (3.9) and (3.8), respectively. These invasion points x_i (circles) divide the spatial domain into several regions. Each one of these regions corresponds to different outcomes of the model (3.1), as x changes from 0 to 1. When $x < x_1$, species 2 dominates the region

to the left of x_1 and the other species are displaced. Species 1 can invade at x_1 (blue circle), and coexistence of species 1 and 2 are possible in the region to the right of x_1. Next, species 3 can invade at x_3 (red circle) and the three competing species can coexist to the right of x_3. This is followed by the extinction of species 2 (x_2: green circle) in which species 2 is excluded and other competitors (species 1 and 3) occupy the region to the right of x_2.

In Figure 3.1A, we observe qualitatively different dynamics of community assembly as x changes. To investigate the differences observed in species presence-absence across locations x, we employed numerical continuation to track the steady states of the model (3.1). As an example, Figure 3.2 shows the steady-state density of species 3 when $\alpha = 0.8$ as x is varied. Our continuation result reveals that the threshold values of x_i observed in Figure 3.1A correspond to transcritical bifurcation points (black points). There are several branches of steady states, particularly stable (blue lines) and unstable (red lines) steady states. As x increases, the existence of different stable steady states are observed: (i) single-species steady state with species 2 present or two-species steady state with species 3 absent (i.e. when $x < x_3$); (ii) three-species steady state (i.e. when $x_3 < x < x_2$); (iii) two-species steady state with species 2 absent (i.e. when $x > x_2$). Transcritical bifurcation occurs at x_i as one steady state exchanges its stability with another steady-state.

Notice that the order of invasion points in Figure 3.1A is as follows: $x_1 < x_3 < x_2$ (assuming x changes from left to right). This means that species 1 invades first, followed by species 3 and then species 2 goes extinct. It is possible to alter the order of which species can invade first by changing the magnitude of environmental gradients ($K_i(x)$). Figure 3.1B serves as an example on the effect of changing $K_3(x)$ from $K_3(x) = 0.9x$ (as in Figure 3.1A) to $K_3(x) = 2x - 0.8$ (as in Figure 3.1B), keeping the other parameter values fixed. According to Figure 3.1B, the order of which species can invade first changes as $K_3(x)$ is altered. Consequently, we have $x_1 < x_2 < x_3$, meaning that after species 1 invades, we can have species 2 goes extinct first and later species 3 invades. This is analogous to the two competing species case (with only one competitor present) and the invasion points (blue, green and red squares) are determined using equation (3.3). In this case, two-species coexistence is possible (e.g. when

$x_1 < x < x_2$ or $x > x_3$ in Figure 3.1B). If the strength of biotic interactions (α) are reduced in Figure 3.1B, three-species coexistence is also possible.

3.4.2 Species Presence-Absence When $\alpha > 1$: Priority Effects

Another point to note is how the qualitative outcomes of the model change as the strength of biotic interactions α is increased. Figure 3.3 depicts the range limits of species predicted by the model (3.1) as the competition coefficient $\alpha = 1.2$. When $\alpha > 1$, this situation leads to alternative stable states and the dynamical behaviour of the model depends on initial abundances of species. Ecologically, alternative stable states are known as priority effects, where species establishment order can determine the presence-absence of species [142], [170]. The initially more abundant species have the potential to predominate and exclude the others [72], [140]. Based on Figure 3.3, we observe that the locations x are separated into several regions; only one species persists in each region, depending on initial abundances. The coexistence of species throughout this region is impossible as aggressive biotic interactions often lead to competitive exclusion of the other species. For instance, species 2 dominates (meaning that this species survives while the other species are excluded) the left side of spatial domain. Then, species 1 survives in the blue region and/or species 3 dominates the red region on the right side of spatial domain, depending on the magnitude of carrying capacities and initial abundances. In this case, the model shows bistable and tristable behaviour, with each steady state at its single-species carrying capacity. Which steady state is reached depends on the initial abundances of species.

In Figure 3.3A, C, E (left column), we observe that competitive exclusion of all but one species occurs with either species 1 or 3 persists on the right-hand region, depending on initial abundances. In contrast to the finding in Figure 3.3B, D, F (right column), it is observed that both species 1 and 3 dominate the right-hand region through priority effects. To explore the robustness of the latter observation, we conducted numerical experiments using environmental gradients described in Figure 3.3A, C, E (i.e. $K_3(x) = 0.9x$) and considered different initial species abundances (e.g. initial abundances favouring each competitor and initial abundances favouring two competitors). In the cases considered, we observe qualitatively similar dynamics to those observed

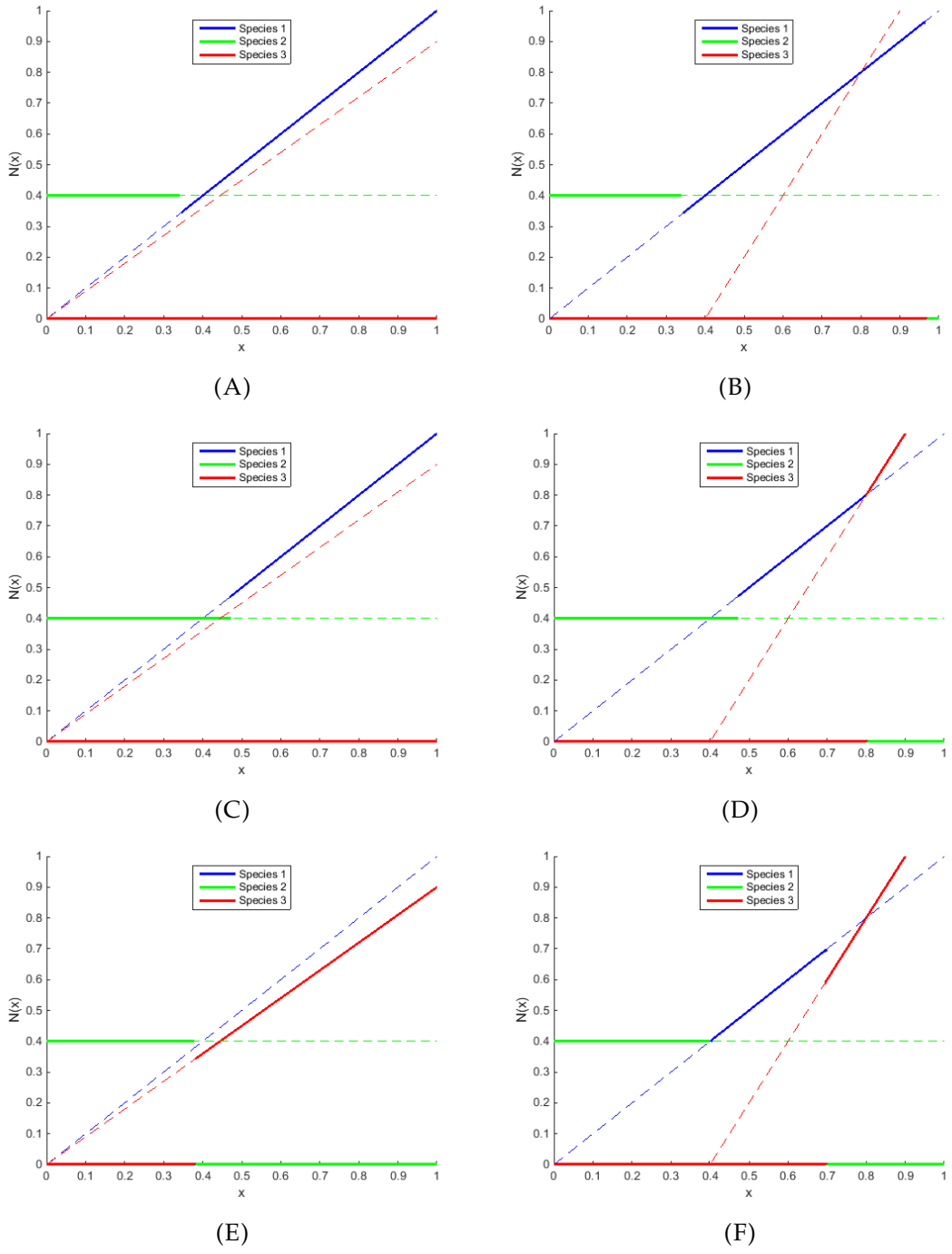
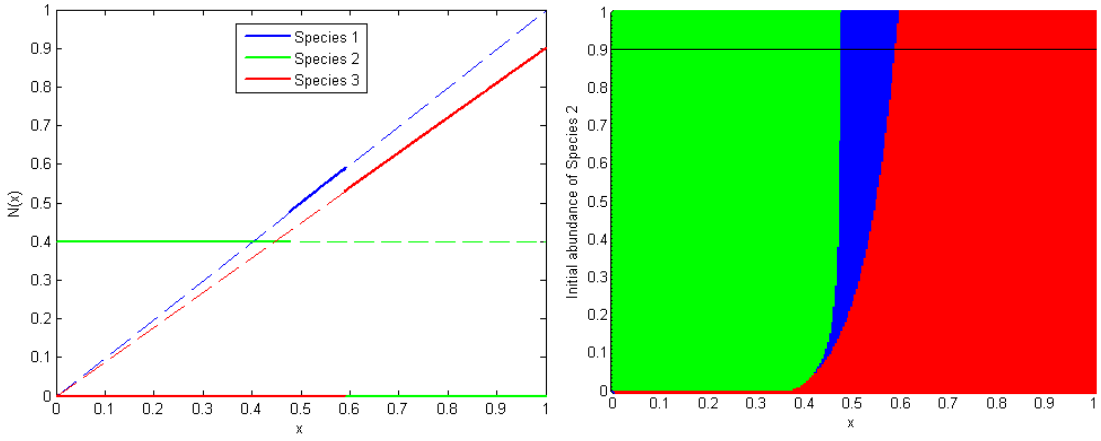


FIGURE 3.3: The steady-state of the model (3.1) with $m = 3$ and $\alpha = 1.2$ following linear environmental gradient (3.2). Carrying capacity of species 3: *Left column*, $K_3(x) = 0.9x$; *Right column*, $K_3(x) = 2x - 0.8$. Solid lines indicate steady-state of $N_i(x)$; dotted lines indicate carrying capacity $K_i(x) = m_i x + c_i$. *First row*, Initial abundances favour species 1: $N_1(x) = 0.9K_1(x), N_2(x) = 0.1K_2(x), N_3(x) = 0.1K_3(x)$. *Second row*, Initial abundances favour species 2: $N_1(x) = 0.1K_1(x), N_2(x) = 0.9K_2(x), N_3(x) = 0.1K_3(x)$. *Third row*, Initial abundances favour species 3: $N_1(x) = 0.1K_1(x), N_2(x) = 0.1K_2(x), N_3(x) = 0.9K_3(x)$. Other parameter values as in Table (3.1). This result is computed using MATLAB `ode45` solver.



(A) (B)

FIGURE 3.4: The steady-state of the model (3.1) with $m = 3$ and $\alpha = 1.2$ following linear environmental gradient (3.2) for the case $K_3(x) = 0.9x$ (this case corresponds to the left column of Figure 3.3). (A) Solid lines indicate steady-state of $N_i(x)$; dotted lines indicate carrying capacity $K_i(x) = m_i x + c_i$. Initial abundances: $N_1(x) = 0.01K_1(x), N_2(x) = 0.9K_2(x), N_3(x) = 0.09K_3(x)$. (B) The graph depicts which species can survive when initial abundances of species 2 (in term of % of K_2) change across x. Blue, green and red coloured areas correspond to the regions dominated by species 1, 2 and 3, respectively. The horizontal black line indicates species presence-absence depicted in (A). Note that the initial abundances of species 1 and 3 and other parameter values are the same as in (A) and Table (3.1). This result is computed using MATLAB `ode45` solver.

in Figure 3.3B, D, F. For example, Figure 3.4A shows the presence-absence of species at $\alpha = 1.2$ predicted by the model (3.1) when $K_3(x) = 0.9x$; this plot is generated using the following initial abundances: $N_1(x) = 0.01K_1(x), N_2(x) = 0.9K_2(x), N_3(x) = 0.09K_3(x)$. To explore potential presence-absence of species for a range of values of initial abundances across locations x, we constructed Figure 3.4B by fixing initial abundances of species 1 and 3 as in Figure 3.4A, and we vary initial abundances of species 2. This plot is coloured blue, green or red depending on which species is present at each location x, with changes in colour corresponding to a range limit of species.

The graph in Figure 3.4B shows how changing the initial abundances of species 2 (in term of % of $K_2(x)$) affects species presence-absence across locations x. The blue, green and red regions indicate the corresponding areas occupied by species 1, 2 and 3, respectively. The width of these regions depend on initial abundances of species 2. For instance, if there is no species 2, then species 3 survives across the whole location x. If species 2 are present at relatively small abundances, then species 2 dominates on the left and only species 3 survives on the right hand part of the region. However, as the initial abundances of species 2 increases, we observe that species 1 can exclude species 3 and

present near the centre (e.g. Figure 3.4A shows the effect at 90% of $K_2(x)$). The width of the blue region occupied by species 1 increases as the initial abundances of species 2 are increased further; this situation affects the regions where species 3 survives near the central region. Based on this finding, we observe that ecologically different species may tip the balance between ecologically similar competitors in unexpected ways, and determine the width of the regions dominated by each species.

3.5 Discussion and Ecological Implications

One of the important cases that we identify is the occurrence of priority effects that can significantly shape species presence-absence. In this situation, competitive exclusion of all but one species occurs. We also find that initial species abundance is a critical feature in determining the range limits of strongly interacting species. Ecologically, this critical feature could be employed as a biocontrol strategy: for instance, consider Figure 3.4B in which we show how the interaction of two ecologically similar species (e.g. species 1 and 3) that compete for common habitats can be controlled by the introduction of an ecologically different competitor (e.g. species 2). If we would like to limit the presence of species 3 near the centre due to its negative effects on the ecosystems while at the same time preserving species 1, then we could potentially use their ecologically different competitor, species 2, as a biocontrol agent. Our result suggests that we could release specified abundances of biocontrol agents, and these agents can reduce the competitive advantage of species 3; consequently, species 3 can be eliminated by species 1 near the central region. The biocontrol agents may tip the balance between the ecologically similar competitors (e.g. species 1 and species 3) and may induce the switch between the single-species steady states (e.g. $(K_1, 0, 0)$ and $(0, 0, K_3)$). In practice, it has been observed through different studies [17], [105], [183] that initial abundances can affect species presence-absence in biological control strategies, and our finding is consistent with these observations. However, in our model, we show that the joint influences of competitive interactions and environmental factors are also necessary in determining species presence-absence.

Based on our findings, we caution that different set of parameter values can result

in different dynamical behaviours as the competitive outcomes also depend on the magnitude of K_i. However, these possible outcomes still correspond to the dynamics of the special case that we discussed above. For instance, we may change the steepness of environmental gradient of species 2 by letting its carrying capacity decreases linearly with x ($m_2 < 0$), instead of assuming a homogeneous distribution ($m_2 = 0$). The change in the K_2 gradients will not move the invasion points by a large distance as there is a rapid change of competitive outcomes. In this case, small changes in model parameters produce small changes in the range limits of species (i.e. mechanism A). Another possible parametrisation to the above special case is when $m_1 > 0$, $m_3 < 0$ and $m_2 = 0$, i.e. two ecologically different species (e.g. species 1 and species 3) competing with another species (e.g. species 2) that can occupy the whole region. In this case, we can expect to observe qualitatively similar dynamics to the above special case as the strength of interspecific competition (α) varies across x.

To summarise, we have employed a deterministic (ordinary-differential equations) model to explore the combined influences of biotic interactions and abiotic environments on the presence-absence of multiple species in this chapter. We find that both biotic and abiotic components determine the range limits of multiple species. Analytical expressions for the range limits of species are derived and and two biological mechanisms that can significantly alter species presence-absence are discussed. Our numerical simulation results demonstrate that competition among multiple species across heterogeneous environments leads to species coexistence or the occurrence of priority effects, depending on the strength of biotic interactions. Overall, our findings indicate that knowledge of species' environmental tolerance, biotic interactions and their initial abundances can improve our ability to predict the presence-absence of species in a multi-species community.

Chapter 4

Local Dispersal and Outcomes of Species Interactions

4.1 Introduction

In Chapter 3, we investigated the effects of biotic interactions on the presence-absence of species across environmental gradients. Without dispersal ($D_i = 0$), we discover that the presence-absence of species depends on the strength of competitive interactions. When $\alpha < 1$ (i.e. interspecific competition is weaker than intraspecific), species can coexist at the same location; when $\alpha > 1$ (i.e. interspecific competition is stronger than intraspecific), priority effects occur with the range limits of species depend on initial abundances. It has also been demonstrated in other studies [69], [70] that biotic interactions are one of the important forces in shaping community assembly, and priority effects can occur in the presence of intense biotic interactions [23]. However, the persistence of priority effects is unclear when dispersal process is incorporated in multi-species communities. Information from two-species system [69], [70] suggest that the occurrence of priority effects is reduced when local dispersal process is considered. Here, we aim to investigate how priority effects interact with local dispersal process and biotic interactions to shape presence-absence of multiple species.

The crucial role of biotic interactions in shaping multispecies communities has long been recognised [36], [64], [75], [100] and is evident in numerous studies [65], [81], [90], [180], [199], [202]. As discussed in Chapter 1, experimental works by Davis et al. [37], [38] illustrate that biotic interactions, dispersal and climate all affect the abundances of three competing fruit fly species as temperature is varied. Urban et al. [186] show how

competition among species and dispersal along elevational gradients can shape multispecies communities. Additionally, the order in which species become established may alter community structure through priority effects [23], [91], [113], [167]. This phenomenon is evident in the presence of intense biotic interactions and high initial abundances of species [39], [66]. However, how the order in which species become established may alter multi-species community dynamics in the presence of local dispersal is not well understood. Specifically, it remains unclear whether the joint influences of dispersal and biotic interactions can lead to the occurrence of priority effects that strongly shape the presence-absence of multiple species.

To address this problem, we extend the deterministic systems discussed in Chapter 3 [133], [164] to model biotic interactions and dispersal among multiple species across heterogeneous environments. To model dispersal between adjacent locations, we incorporate a local dispersal process as described in Chapter 2 into our systems. This inclusion leads to a system of partial-differential equations (PDE) consisting of interspecific competition, environmental suitability (carrying capacity) and local dispersal terms. We investigate the joint effects of local dispersal and biotic interactions on community dynamics by comparing simulation results of the models with and without dispersal. We find that dispersal can substantially expand species ranges when biotic and abiotic forces are present; consequently, coexistence of multiple species is possible. Our models also exhibit ecologically interesting priority effects, mediated by biotic interactions. As discussed in Chapter 3, priority effects emerge in the presence of intense biotic interactions; in the absence of dispersal, competitive exclusion of all but one species occurs (i.e. coexistence is impossible). We demonstrate that dispersal reduces competitive exclusion effects that occur in no-dispersal case and promotes coexistence of multiple species. Our simulation results also show that priority effects are still evident in multi-species communities when dispersal is incorporated into the models. To investigate the occurrence of this phenomenon and gain better understanding of the system dynamics, we employ numerical continuation to track both stable and unstable steady states as parameter is varied in the models. We illustrate the existence of threshold values of competitive strength (i.e. transcritical bifurcations), which results in different species presence-absence in multi-species communities with and without

local dispersal. In the case of priority effects, this bifurcation point indicates a threshold value in the strength of biotic interactions above which alternative stable states occur.

4.2 A Deterministic Model with Biotic Interactions and Local Dispersal

We consider a partial differential equation (PDE) model for the densities $N_i\,(x,\ t)$ of m species in a one-dimensional domain $0 \leq x \leq 1$:

$$\frac{\partial N_i}{\partial t} = \frac{r_i N_i}{K_i(x)}\left(K_i(x) - \sum_{j=1}^{m} \alpha_{ij} N_j\right) + D_i \frac{\partial^2 N_i}{\partial x^2} \qquad (i = 1, 2, ..., m) \tag{4.1}$$

where r_i is the intrinsic growth rate, K_i is the carrying capacity and D_i is the diffusion coefficient of species i, and α_{ij} is the coefficient for competition of species j on species i. By rescaling the density of species i relative to its intraspecific competition coefficient α_{ii}, we may effectively set the intraspecific competition coefficients α_{ii} to equal 1, and the remaining competition coefficients α_{ij} represent the ratio of intraspecific to interspecific competition. Equation (4.1) is a spatially extended Lotka-Volterra competition model [23], [69], [164], which becomes a PDE with the addition of the diffusion term.

The diffusion term models dispersal among locations, with the parameter D_i representing the strength of dispersal for species i. We assume that interacting species have the same dispersal rate ($D_i = D$) and no migration occurs across boundaries (by imposing zero-flux boundary conditions for each species):

$$D_i \frac{\partial N_i}{\partial x}\bigg|_{x=0,1} = 0. \tag{4.2}$$

4.2.1 Numerical Methods

Equation (4.1) with zero-flux boundary conditions (4.2) is solved numerically using MATLAB `pdepe` solver. `pdepe` solves systems of PDE in one spatial variable x and time t using the method of lines. In the method of lines, the spatial domain $0 \leq x \leq 1$ is divided into a mesh with $A + 1$ equally spaced nodes $x_j = jh$ for $j = 0, 1, ..., A$, where $h = \frac{1}{A}$ is the uniform mesh size. The spatial derivative in equation (4.1) is replaced by

a second central difference approximation:

$$\frac{\partial^2 N_j}{\partial x^2} = \frac{N_{j+1} - 2N_j + N_{j-1}}{h^2} \tag{4.3}$$

This leads to a system of $3(A+1)$ ODE, one for the density of each species at a series of equally spaced x points. `pdepe` then solves the resulting system of ODE by a standard ODE solver, `ode15s` for $t = 1000$. We used $h = 2 \times 10^{-3}$ and initial conditions as indicated in each figure section. The results are insensitive to a reduction in grid spacing h.

We also verified that steady state is stable. To do this, the time derivative in equation (4.1) is set to zero and the spatial derivative in equation (4.1) is replaced by a second central difference approximation (4.3), with constant mesh size h. The zero-flux boundary conditions (4.2) are coded in the equations for the end points using a finite difference approximation. This results in a system of $3(A+1)$ non-linear equations, one for the density of each species at a series of uniformly spaced x points, $x_j = jh$ for $j = 0, 1, ..., A$, where $h = \frac{1}{A}$. This system is solved for steady state using MATLAB `fsolve` with initial guess is the same as initial condition indicated in each figure section. To determine the stability of steady state, the Jacobian matrix is calculated numerically in `fsolve` and then the eigenvalues are computed using `eig` function. The steady state is stable if all eigenvalues have negative real parts.

We also used numerical continuation package XPPAUT to check our simulation results. As usual, equation (4.1) is discretised using the method of lines with the spatial derivative in equation (4.1) is replaced by a second central difference approximation (4.3), with constant mesh size h. The zero-flux boundary conditions (4.2) are coded in the equations for the end points using a finite difference approximation. This yields a system of ODE, which is solved for steady state in XPP using `cvode` solver for $t = 1000$. Then, the steady state is continued in AUTO, in which we tracked stable and unstable steady states and also bifurcation points as a model parameter changes. Continuation results shown in this chapter used a maximum/minimum allowable step size of parameter, $10^{-1}/10^{-6}$.

4.3 Results

In this section, we compare the simulation results of the model (4.1) with ($D_i > 0$) and without ($D_i = 0$) dispersal. To determine the presence-absence of species across locations x, we define a species to be present if its density is greater than 0.5% of the maximum observed density of that species [61], [162], [163]. This can be thought of as a detection threshold (i.e. meaning that we would not observe a species that is present at a sufficiently low density).

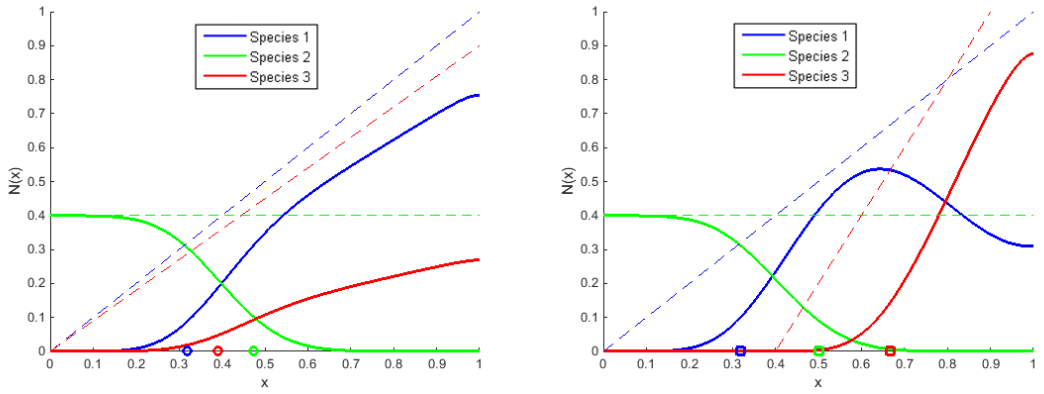
Based on these results, we discuss the effects of local dispersal on the range limits of species when biotic and abiotic factors are present. Additionally, we also present some numerical continuation results in order to explain the differences observed in species presence-absence as the strength of biotic interactions α changes.

4.3.1 The Effects of Local Dispersal When $\alpha < 1$

One of the important effects of dispersal is to allow species to be present in otherwise unsuitable locations (i.e. compared to no-dispersal case). This effect can be illustrated by Figure 4.1 as an example when $\alpha < 1$. In contrast to species range limits observed in no-dispersal case (i.e. x_i), inclusion of dispersal increases the densities of species the left and/or right of x_i (with x_i corresponds to circles and squares in Figure 4.1A, B). Dispersal also causes the zone of two-species and three-species coexistence (compare Figure 4.1A with Figure 3.1A) to increase. We also observe that inclusion of dispersal into the model (4.1) enhances the spatial extent of multi-species coexistence compared to no-dispersal case (compare Figure 4.1B with Figure 3.1B).

4.3.2 The Effects of Local Dispersal When $\alpha > 1$

Without dispersal ($D_i = 0$) and in the presence of intense biotic interactions (i.e. when $\alpha > 1$), we observe priority effects. In this case (Figure 3.3), competitive exclusion occurs with only one species surviving at any given location, and the species range limits depend on initial abundances. Inclusion of dispersal ($D_i > 0$) reduces competitive exclusion (of all but one species) effects that occur in no-dispersal case and promotes coexistence of species. This situation is illustrated by Figure 4.2: because of dispersal,



(A) $K_3(x) = 0.9x$ (B) $K_3(x) = 2x - 0.8$

FIGURE 4.1: The steady-state of the model (4.1) with $m = 3$, $D = 0.001$ and $\alpha = 0.8$ following linear environmental gradient (3.2). Carrying capacity of species 3: (A) $K_3(x) = 0.9x$ to (B) $K_3(x) = 2x - 0.8$. Solid lines indicate steady-state of $N_i(x)$; dotted lines indicate carrying capacity $K_i(x) = m_i x + c_i$. Circles and squares show the locations of the invasion points x_i in no-dispersal case (with equations (3.5), (3.8) and (3.9) represent the invasion points of species, x_1 , x_3 and x_2, respectively for (A); and equation (3.3) can be used to determine x_i for (B)). Initial abundances: $N_1(x) = 0.9K_1(x)$, $N_2(x) = 0.1K_2(x)$, $N_3(x) = 0.1K_3(x)$. Other parameter values as in Table (3.1). This result is computed using MATLAB `pdepe` solver.

multiple species coexist near the central region in the presence of intense biotic interactions (compare Figure 4.2 with Figure 3.3). However, priority effects are still evident (compare Figure 4.2 C with E; and Figure 4.2 B with D) with the inclusion of dispersal into the model (4.1); we observe that either one- or multiple-species can survive at any location x depending on initial abundances.

To understand the dynamical behaviour of equation (4.1) for a range of values of the competition coefficient α across locations x, we constructed summary plots of the models using environmental gradients described in Figure 4.2A, C, E (left-column). Similar summary plots can also be constructed for the environmental gradients described in Figure 4.2B, D, F (right-column). These summary plots are shown in Figure 4.3A (no-dispersal, $D = 0$) and Figure 4.3B (inclusion of dispersal, $D = 0.001$). These plots depict which combination of species is present at each location x and are generated using three different initial abundances, each favouring one of the three species. Different colours represent different combinations of species presences. Changes in colour correspond to a range limit of at least one species. As discussed earlier, we employed 0.5% detection threshold (i.e. 0.5% of the maximum observed density of that species [61], [162], [163]) in order to determine the presence-absence of species across location x. We

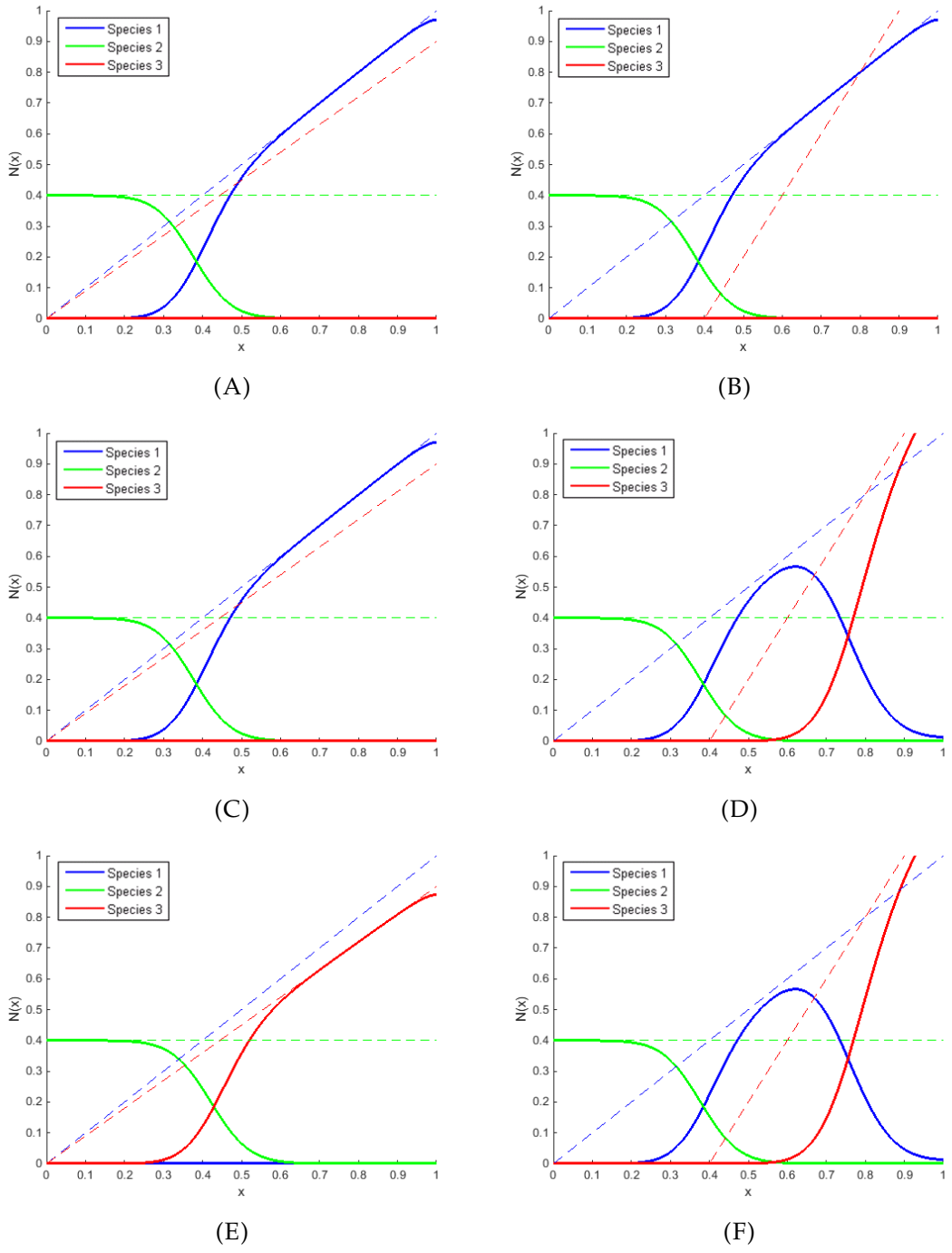
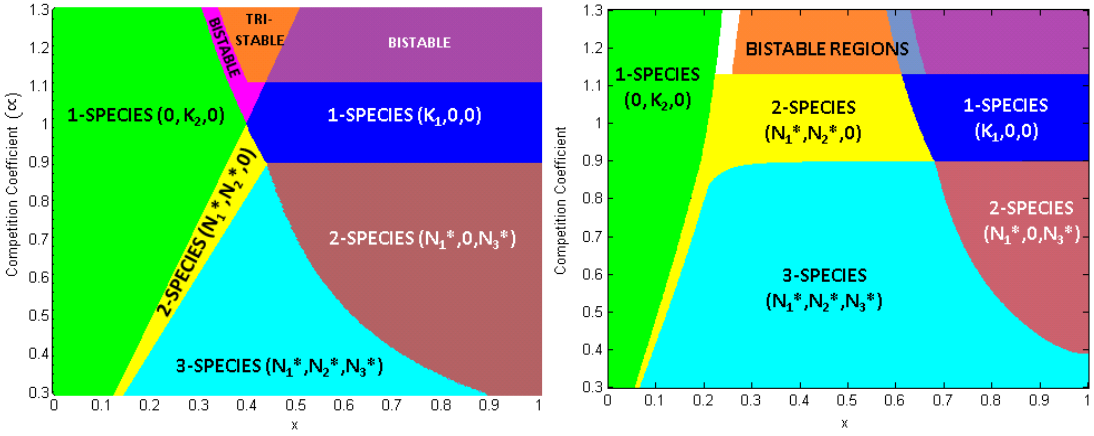


FIGURE 4.2: The steady-state of the model (4.1) with $m = 3$, $D = 0.001$ and $\alpha = 1.2$ following linear environmental gradient (3.2). Carrying capacity of species 3: *Left column*, $K_3(x) = 0.9x$; *Right column*, $K_3(x) = 2x - 0.8$. Solid lines indicate steady-state of $N_i(x)$; dotted lines indicate carrying capacity $K_i(x) = m_i x + c_i$. *First row*, Initial abundances favour species 1: $N_1(x) = 0.9K_1(x), N_2(x) = 0.1K_2(x), N_3(x) = 0.1K_3(x)$. *Second row*, Initial abundances favour species 2: $N_1(x) = 0.1K_1(x), N_2(x) = 0.9K_2(x), N_3(x) = 0.1K_3(x)$. *Third row*, Initial abundances favour species 3: $N_1(x) = 0.1K_1(x), N_2(x) = 0.1K_2(x), N_3(x) = 0.9K_3(x)$. Other parameter values as in Table (3.1). This result is computed using MATLAB `pdepe` solver.



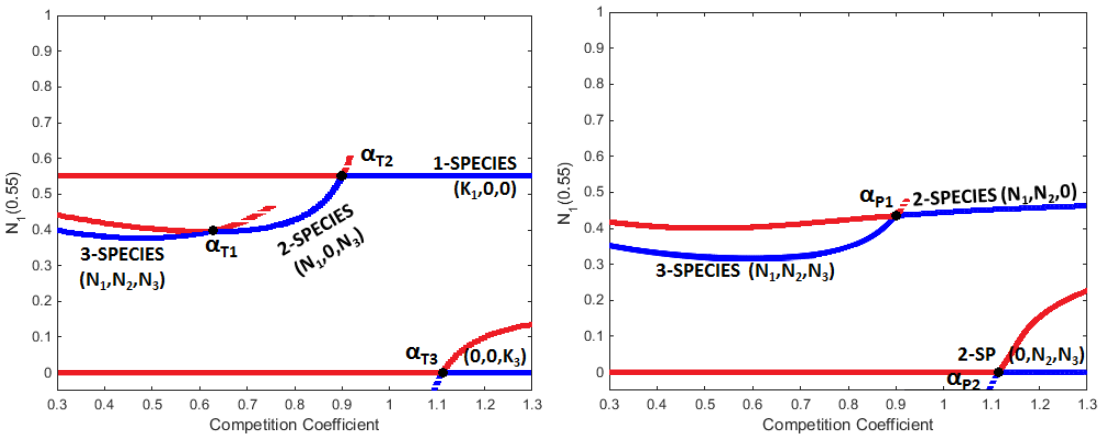
(A) No-dispersal ($D = 0$) (B) Inclusion of dispersal ($D = 0.001$)

FIGURE 4.3: Summary plots of the model (4.1) when $m = 3$, following linear environmental gradient (3.2) with carrying capacity of species 3, $K_3(x) = 0.9x$: (A) $D = 0$; (B) $D = 0.001$. Colours correspond to combinations of species presences as described in the figure; for priority effects case: (A) *pink*, $(K_1, 0, 0)$ or $(0, K_2, 0)$; *purple*, $(K_1, 0, 0)$ or $(0, 0, K_3)$; *orange*, $(K_1, 0, 0)$ or $(0, K_2, 0)$ or $(0, 0, K_3)$; (B) *white*, $(N_1, N_2, 0)$ or $(0, K_2, 0)$; *orange*, $(N_1, N_2, 0)$ or $(0, N_2, N_3)$; *dark grey*, $(K_1, 0, 0)$ or $(0, N_2, N_3)$; *purple*, $(K_1, 0, 0)$ or $(0, 0, K_3)$. Other parameter values as in Table (3.1). These plots are computed by numerical simulation with MATLAB `pdepe` solver.

have also investigated the outcomes of the models using various ecological criteria (e.g. 0.5% of the maximum carrying capacity of that species, $K_{i,max}$; 0.5% of the maximum density of any species; and 0.5% of the maximum total density of species); the results presented in this section are robust to reasonable choices of presence-absence criterion.

No dispersal. Figure 4.3A depicts the summary plot for the range limits of species predicted by the model (4.1) with no dispersal ($D_i = 0$), as the strength of biotic interactions α and location x change. In the absence of dispersal and when $\alpha < 1$, coexistence of two (brown and yellow regions) or three-species (cyan colour) is possible near the centre of the region. However, when $\alpha > 1$, this situation leads to the occurrence of priority effects. In this case, the model (4.1) shows bistable (pink and purple regions) and tristable (orange region) behaviour, with each steady state at its single-species carrying capacity. Which steady state is reached depends on the initial abundances of species.

Inclusion of dispersal. Figure 4.3B illustrates the presence-absence of species in the model (4.1) with dispersal. Overall, a major effect of dispersal is to increase local coexistence. When $\alpha < 1$, dispersal causes the zone of two-species (yellow regions) and three-species coexistence (cyan region) to increase compared to no-dispersal case (Figure 4.3A). When $\alpha > 1$, dispersal weakens competitive exclusion effects that occur in



(A) No-dispersal ($D = 0$) (B) Inclusion of dispersal ($D = 0.001$)

FIGURE 4.4: The density of a focal species (species 1) at $x = 0.55$ for the model (4.1) when $m = 3$ as competitive strength α changes: (A) $D = 0$; (B) $D = 0.001$. Linear environmental gradient (3.2) with carrying capacity of species 3, $K_3(x) = 0.9x$. The threshold values α_T and α_P correspond to transcritical bifurcation points (black points) for the ODE and PDE models, respectively. Blue and red curves indicate stable and unstable steady-states as described in the figure. Solid and dotted curves indicate ecologically feasible solution and infeasible solution (i.e. one of the densities of species is negative). Other parameter values as in Table (3.1). This plot is computed by numerical continuation using XPPAUT.

no-dispersal case and promotes coexistence of species. Inclusion of dispersal into the model leads to replacement of single-species steady states (pink, purple and orange regions in Figure 4.3A) with single- and multiple-species steady states (white, orange, dark grey and purple regions in Figure 4.3B). We also observe that priority effects are still evident with the inclusion of local dispersal process.

4.3.3 Theoretical Explanations of Different Species Presence-Absence in the Models with and without Dispersal

We observe qualitatively different dynamics between the modelling results with ($D_i > 0$) and without ($D_i = 0$) dispersal (Figure 4.3). To investigate the differences observed in species presence-absence across locations x as competitive strength α changes, we employed numerical continuation to track the steady states of the model (4.1). For instance, Figure 4.4A (respectively, Figure 4.4B) shows the steady-state density of species 1 (N_1) at $x = 0.55$ when $D = 0$ (respectively, $D = 0.001$) using environmental gradients described in Figure 4.2A, C, E (left-column), as competition coefficient α is varied. Similar graphs could be plotted for N_2 and N_3.

No dispersal. The summary plot in Figure 4.3A shows that there are critical values for competitive strength α, which result in different combinations of species presences. Our continuation result in Figure 4.4A reveals that the observed critical values of α in the summary plot Figure 4.3A correspond to transcritical bifurcation points (i.e. α_{T1}, α_{T2} and α_{T3}). Based on Figure 4.4A, there are several branches of steady states, particularly stable (blue curves) and unstable (red curves) steady states. As α increases near the central region, the existence of different stable steady states are observed: (i) three-species steady state (i.e. when $\alpha < \alpha_{T1}$); (ii) two-species steady state with species 2 absent (i.e. when $\alpha_{T1} < \alpha < \alpha_{T2}$); (iii) single-species steady state with species 1 present (i.e. when $\alpha_{T2} < \alpha < \alpha_{T3}$). When $\alpha > \alpha_{T3}$, priority effects occur; in this case, there are two stable steady-states (blue curves): species 1 at its single species steady state and species 3 at its single species steady state; these are separated by an unstable two-species steady state (red curve); which of the two steady states is reached depends on initial abundances.

Inclusion of dispersal. We observe that there occurs critical values of α in the summary plot (Figure 4.3B), which result in different species presence-absence. By employing continuation methods (Figure 4.4B), we show that these threshold competition coefficients (α_{P1} and α_{P2}) correspond to transcritical bifurcation points. Overall, there are several branches of steady states: the upper (two-species coexistence with species 3 absent), middle (three-species coexistence) and lower branches (two-species coexistence with species 1 absent) of steady states are stable (blue curves); there is unstable (three-species) steady state (red curve) separating the upper and lower branches of stable steady states. When $\alpha < \alpha_{P1}$, we observe that three-species steady state is stable; when $\alpha_{P1} < \alpha < \alpha_{P2}$, we find that two-species steady state with species 3 absent is stable. We also discover that the bifurcation point α_{P2} indicates a threshold value in competitive strength beyond which priority effects occur; for $\alpha > \alpha_{P2}$, the density N_1 tends toward upper or lower steady-state (blue curves), depending on initial species abundances.

4.4 Discussion and Ecological Implications

The presence-absence of species is affected by abiotic environmental conditions, biotic interactions and local dispersal. We have used partial differential equation models to study the combined influences of dispersal and biotic interactions among multiple species across heterogeneous environments. The presence-absence of species depends on both the magnitude of dispersal and strength of biotic interactions.

Our simulation results show that without dispersal, the models exhibit priority effects when $\alpha > 1$. In this situation, one species eliminates the other species in mutually suitable environments; initial abundances affect presence-absence and range limits are hard to predict. This sensitivity is softened by including dispersal into the models where competitive exclusion effects that occur in no-dispersal case is weakened; as a result, dispersal promotes coexistence of multiple species near range-limits. These observations are in agreement with the findings of several studies: dispersal can allow species to be present in otherwise unsuitable locations [37], [38], [69], [159] and expand their range limits [48]; consequently, species diversity is enhanced, with multiples species can coexist due to dispersal [9], [23], [122].

While it has been illustrated that dispersal reduces the effects of competitive exclusion and promotes species coexistence, our results also demonstrate the persistence of priority effects in a multi-species community assembly. This finding is contrast with the observation of some studies of two-species system [69], [70], which show that considering local dispersal process in predicting species range limits can lead to reduction of priority effect phenomenon. Based on our results, we suggest that priority effects are still evident in multi-species ecosystems and this situation can strongly determine species range limits. Due to these reasons, this phenomenon warrants further study and will be the focal point of our investigation in Chapter 5, Chapter 6 and Chapter 7.

To gain better understanding of the systems dynamics and investigate the occurrence of priority effects, we also perform numerical continuation to track both stable and unstable steady states as a model parameter is varied. Continuation result (Figure 4.4) suggests a theoretical explanation for the observed differences in species

presence-absence in our simulation results, and also in a number of different studies [23], [69], [70]; we find that there are threshold values for competitive strength, which correspond to transcritical bifurcations in the models with and without dispersal. Based on these bifurcation points, we characterise the bifurcation scenarios that give rise to several outcomes of species interactions (e.g. stable coexistence, competitive exclusion and priority effects), as discussed by some studies [23], [69], [70].

In short, this study illustrates the significant roles local dispersal and biotic interactions in shaping range limits of species. Overall, our work provides some insights on the possible explanations of species range limits, especially from the theoretical point of views. More investigation is needed into this topic, particularly in the case of priority effects, because this phenomenon can induce an uncertainty in the predictions of community dynamics. Therefore, for future works, we aim to investigate the interaction of priority effects with other ecological processes such as dispersal process, demographic stochasticity and abiotic environments.

Chapter 5

Stochasticity, Local Dispersal and Priority Effects

5.1 Introduction

In this chapter, we address the following questions:

- When does the order in which species become established (i.e. priority effects) matter in determining the presence-absence of species and when does this phenomenon depend on local dispersal process?
- How does demographic stochasticity affect the occurrence of priority effects in multi-species community assembly?

These are important questions in ecology [23], [167] and are crucial in order to produce robust predictions about which species will be present (or absent) across a geographical region [61], [167], [199]. Some predictive models concentrate on the influence of environmental variables [112], [157], [169], [173] and biotic interactions [23], [67], [69], [199] on presence-absence of species, yet dispersal [11], [13], [60], [167] and demographic stochasticity [62], [95], [171] can also affect the dynamics of natural communities. For instance, Holt et al. [95] find that the ecological processes such as dispersal and stochasticity can have different effects on the range limits of species: while dispersal can elevate species abundance and reduce the possibility of species extinction due to stochasticity, it has also been demonstrated that dispersal can at times reduce population size and thus enhance extinction risk. Given these contrasting observations, the joint effect of local dispersal and stochasticity on multi-species community dynamics is

not well understood in the presence of priority effects, which are mediated by intense biotic interactions.

Generally, ecological processes such as dispersal and growth can be described at the individual level or at the population level [5], [41], [149], [161], [198]. In Chapter 4, we have looked at interacting species from the population-level perspective and modelled them as continuous densities; in this case, species presence-absence can be predicted using deterministic models [149], [161], [198]. Alternatively, if the interacting species are represented as collections of discrete individuals and stochastic events (e.g. birth and death) are considered, their locations can be simulated using stochastic individual-based models (IBM) [120], [149], [161], [197], [198]. In the ecological context, IBMs have been defined as "simulation models that treat individuals as unique and discrete entities which have at least one property in addition to age that changes during the life cycle" [74]. Even though there are several models used in ecology that do not entirely satisfy this definition, they can still be referred to as IBM as long as they treat individuals as discrete entities [44], [132]. In some applications, these types of models are known as stochastic compartmental models. In parallel with common usage in ecology, we classify our stochastic model as an IBM. By employing these two modelling frameworks, we investigate the interaction of priority effects with dispersal and stochasticity in shaping presence-absence of species.

We first employ deterministic PDE model as in Chapter 4 with bounded ecological niches for species: one way to model such an ecological niche consists in considering that the environment is inhospitable to interacting species outside the boundaries of their fundamental niches. Consider elevation gradients as an example: due to species fundamental niches are bounded by the ends of the environmental gradient, empirical studies have shown that the density of some species may peak at intermediate elevation [77], [115]. Motivated by these observations, we incorporate non-linear environmental gradients (i.e. carrying capacity varies nonlinearly with spatial locations) into our models. By employing this deterministic model, we investigate the conditions under which priority effects occur and disappear as dispersal intensity changes in a multi-species community. To investigate what impact demographic stochasticity and local dispersal will have on community assembly in the presence of priority effects,

we develop a comparable stochastic IBM that captures the dynamics at an individual scale. In the IBM, each individual from each species is an agent that is tracked explicitly over time while undergoing a birth-death-movement process [42], [44], [50]. We aim to explore the occurrence of priority effects in our stochastic IBM by considering various dispersal scenarios and different population sizes, and to check whether the range-limit predictions are similar using the stochastic and deterministic models.

The chapter is organised as follows. After describing the two models, we show conditions under which dispersal first enhances priority effects (i.e. for moderate dispersal), and then leads to their reduction (i.e. for strong dispersal) in a multi-species community. We then demonstrate the agreement between deterministic models and IBM for large populations, but disagreement for small populations. Additionally, we also illustrate more (respectively, fewer) occurrences of priority effects in IBM for large (respectively, small) populations as dispersal strength changes. Finally, we discuss several ecological implications of our results.

5.2 The Models

5.2.1 Population-Level (Deterministic) Model

We consider a partial differential equation (PDE) model for the densities $N_i\,(x,\ t)$ of m species in a one-dimensional domain $0 \leq x \leq 1$:

$$\frac{\partial N_i}{\partial t} = \frac{r_i N_i}{K_i(x)}\left(K_i(x) - \sum_{j=1}^{m} \alpha_{ij} N_j\right) + D_i \frac{\partial^2 N_i}{\partial x^2} \qquad (i = 1, 2, ..., m) \tag{5.1}$$

where r_i is the intrinsic growth rate, K_i is the carrying capacity and D_i is the diffusion coefficient of species i, and α_{ij} is the coefficient for competition of species j on species i. As in previous chapter, we rescale the density of species i relative to its intraspecific competition coefficient α_{ii} and we set the intraspecific competition coefficients α_{ii} to equal 1; thus, the remaining competition coefficients α_{ij} represent the ratio of intraspecific to interspecific competition. Equation (5.1) is a spatially extended Lotka-Volterra competition model [23], [69], [164], which becomes a PDE with the addition of the diffusion term.

The suitability of a particular environment or location is modelled by incorporating a spatial dependence x into the carrying capacity term; each species' carrying capacity $K_i(x)$ can vary with spatial location x. x could be a location within a geographical region, or used as a proxy for representing abiotic environmental factors such as temperature, moisture or elevation that affect the carrying capacity of species. The effects of biotic interactions on range limits can depend on how each species responds to the environmental gradient. While we could use a linear function for carrying capacity as discussed in Chapter 3 and Chapter 4, there can be two limitations of this kind of function [69], [70]: (i) carrying capacity changes unboundedly as x varies; (ii) theoretically, species' fundamental niches extend for an infinite distance. These limitations can be removed using nonlinear environmental gradients (i.e. carrying capacity varies nonlinearly with x). In particular, we employ the following quadratic function:

$$K_i\left(x\right) = \max\left\{K_{i,max}\left(1 - \frac{(x - x_i)^2}{w_i^2}\right), 0.001\right\} \tag{5.2}$$

where x_i is the location at which the carrying capacity for species i is at its maximum $K_{i,max}$ and w_i is the width of the fundamental niche. To ensure equation (5.1) is well defined, we set $K_i(x)$ to a small but non-zero value (0.001) outside the fundamental niche. Other types of function for the carrying capacity could also be chosen, for example a Gaussian function. For visualisation of carrying capacity described by equation (5.2), refer to Figure 5.1A.

The diffusion term models dispersal among locations, with the parameter D_i representing the strength of dispersal for species i. We assume that interacting species have the same dispersal rate ($D_i = D$) and no migration occurs across boundaries (by imposing zero-flux boundary conditions for each species):

$$D_i \frac{\partial N_i}{\partial x}\bigg|_{x=0,1} = 0. \tag{5.3}$$

5.2.2 Individual-Level (Stochastic) Model

To investigate how the underlying population-level information relates to a smaller individual scale, we develop a stochastic IBM, which is constructed to be comparable

TABLE 5.1: Parameter values.

Symbol	Description	Population Size	
		Large	Small
r_i	The intrinsic growth rate of species i	1	1
$K_{1,max}$	Maximum carrying capacity of species 1	4000	400
$K_{2,max}$	Maximum carrying capacity of species 2	5000	500
$K_{3,max}$	Maximum carrying capacity of species 3	5000	500
x_1	The most favourable location for species 1	0.8	0.8
x_2	The most favourable location for species 2	0.2	0.2
x_3	The most favourable location for species 3	0.5	0.5
w_1	The width of the fundamental niche for species 1	0.6	0.6
w_2	The width of the fundamental niche for species 2	0.7	0.7
w_3	The width of the fundamental niche for species 3	0.25	0.25
D_i	Diffusion coefficient	0-0.0015	0-0.0015
Δx	Space step	0.01	0.01
Δt	Time step	0.0001	0.0001
v_i	Probability of moving left or right (equation (5.4))	0.001	0.001
α	Competition coefficient (values given in figure captions)		

with the deterministic model: equation (5.1) is the mean-field equation for the stochastic IBM in the limit $\Delta x, \Delta t \to 0$ with $(\Delta x)^2/\Delta t$ held constant and the population size is sufficiently large. Now, assume that we have a one-dimensional lattice and each individual can reproduce, die or move one lattice site to the left or right following an unbiased random walk. As discussed in Section 2.4.1, random walk theory [29] gives the relationship between the probability v_i that an individual moves a short distance Δx at each time step Δt in the stochastic IBM, with the diffusion coefficient D_i in the deterministic model (5.1):

$$D_i = \frac{v_i(\Delta x)^2}{\Delta t} \tag{5.4}$$

Now define $n_i\,(x,\ t)$ as the number of individuals of species i at location x and time t, where $n_i = N_i \Delta x$ and $n_i \in \{0, 1, 2, ...\}$. To model the stochastic birth-death process, let the per-capita birth rate be r_i and the per-capita death rate be μ_i. Comparing with the deterministic model (5.1), the death rate $\mu_i(x,t) = \frac{r_i}{K_i(x)} \sum_{j=1}^{m} \alpha_{ij} N_j(x,t)$. We set $\Delta t = 0.0001$ and $\Delta x = 0.01$, and we checked that these choices of Δt and Δx satisfy the condition $\Delta t \ll 1/\lambda$, where λ is the aggregate rate of all types of transitions for species i at a given lattice site. This can be done by checking the sum of probabilities during simulations so that this quantity does not exceed 1. The possible types of transition for each species at each site are then: birth (with probability $r_i n_i(x,t)\Delta t$); death (with

probability $\mu_i(x,t)n_i(x,t)\Delta t$); move left or right (with probability $v_i n_i(x,t)$, with v_i from equation (5.4)). At the right boundary at $x = 1$ (respectively left boundary at $x = 0$), each individual is unable to move right (respectively left). Thus, we have a 'reflecting barrier', which is analogous to the no-flux boundary conditions in equation (5.3)[161]. Changes in state are not actioned until the following time step, when all sites are simultaneously updated.

5.2.3 Numerical Methods

Numerical simulations are conducted for the stochastic IBM and deterministic models and the results of the two models are compared in the next sections. For the deterministic models, equation (5.1) with zero-flux boundary conditions (5.3) is solved numerically using MATLAB `pdepe` solver. `pdepe` solves systems of PDE in one spatial variable x and time t using the method of lines. In the method of lines, the spatial domain $0 \leq x \leq 1$ is divided into a mesh with $A+1$ equally spaced nodes $x_j = jh$ for $j = 0, 1, ..., A$, where $h = \frac{1}{A}$ is the uniform mesh size. The spatial derivative in equation (5.1) is replaced by a second central difference approximation (4.3). This leads to a system of $3(A+1)$ ODE, one for the density of each species at a series of equally spaced x points. `pdepe` then solves the resulting system of ODE by a standard ODE solver, `ode15s` for $t = 1000$. We used $h = 2 \times 10^{-3}$ and initial conditions as indicated in each figure section. The results are insensitive to a reduction in grid spacing h.

We also verified that steady state is stable. To do this, the time derivative in equation (5.1) is set to zero and the spatial derivative in equation (5.1) is replaced by a second central difference approximation (4.3), with constant mesh size h. The zero-flux boundary conditions (5.3) are coded in the equations for the end points using a finite difference approximation. This results in a system of $3(A+1)$ non-linear equations, one for the density of each species at a series of uniformly spaced x points, $x_j = jh$ for $j = 0, 1, ..., A$, where $h = \frac{1}{A}$. This system is solved for steady state using MATLAB `fsolve` with initial guess is the same as initial condition indicated in each figure section. To determine the stability of steady state, the Jacobian matrix is calculated numerically in `fsolve` and then the eigenvalues are computed using `eig` function.

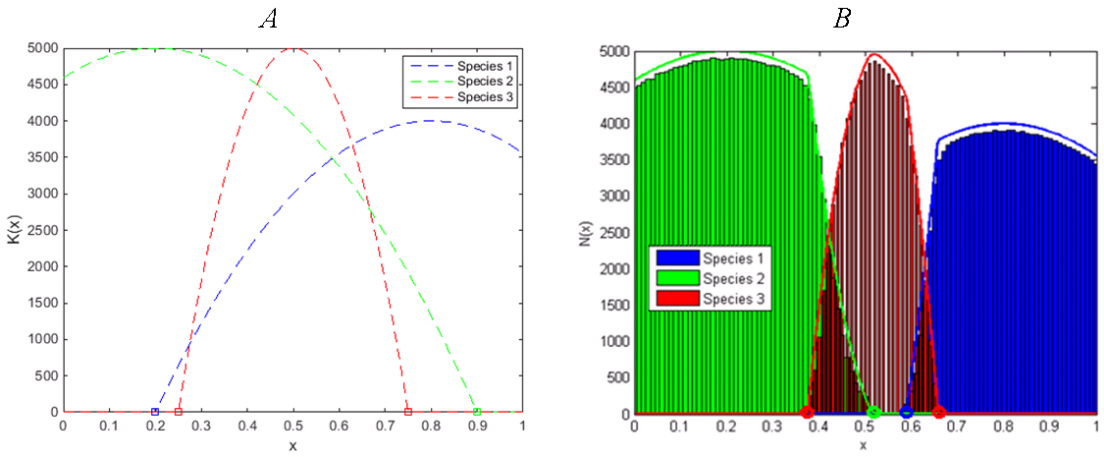


FIGURE 5.1: *A*, The nonlinear carrying capacities (dotted lines) following equation (5.2) for species 1 (blue), species 2 (green) and species 3 (red) with squares representing the range limits of species in the absence of biotic interactions. *B*, Results of the deterministic models (solid lines) and averaged realisations of the stochastic IBM (bar graphs) with circles representing the range limits of species in the presence of biotic interactions. Competition coefficient: $\alpha_{ij} = 0.85$. Dispersal rate: $D_i = 0$. Other parameter values as in Table (5.1).

The steady state is stable if all eigenvalues have negative real parts. Unless otherwise stated, parameter values used in the simulation are given in Table (5.1).

5.3 Results

In the absence of dispersal ($D_i = 0$), we have shown in Chapter 3 that species presence-absence depends on the competitive strength α. When $\alpha < 1$ (i.e. interspecific competition is weaker than intraspecific), species can coexist at the same location; for instance, Figure 5.1B shows the deterministic and stochastic predictions with no dispersal when $\alpha < 1$, with local coexistence of species are possible near the central region. Competition from species 2 (green) and species 3 (red) eliminates species 1 (blue) from some locations x and shifts the range limit of species 1 from $x = 0.2$ (blue square, Figure 5.1A) to the right (blue circle, Figure 5.1B); similarly, the range limits of species 2 (green circle) and species 3 (red circles) are affected due to biotic interactions.

It has also been demonstrated in Chapter 3 that when $\alpha > 1$ (i.e. interspecific competition is stronger than intraspecific), priority effects occur with the range limits of species depend on initial abundances. Without dispersal, we observe that coexistence of species is impossible. As discussed in Chapter 4, inclusion of dispersal ($D_i > 0$) reduces priority effects and prevents competitive exclusion phenomenon that occurs in

no-dispersal case. In the following sections, we will show different effects of dispersal on community dynamics: dispersal can either enhance priority effects and promote coexistence of species, or dispersal can cause priority effects to disappear. We also highlight the similarities and differences between the predictions from deterministic and stochastic simulations, with respect to the occurrence of priority effects on range limits of species.

5.3.1 The Effects of Dispersal on the Occurrence of Priority Effects in the Deterministic Models

We performed numerical simulation of the deterministic model (5.1) to investigate the occurrence of priority effects when $\alpha > 1$ using various initial abundances favouring different species, and considering several dispersal scenarios. In particular, we started by exploring the effects of changing initial abundances on priority effects in no-dispersal case ($D_i = 0$) and we plotted the density of species across locations x; without dispersal, the dynamics are governed by the ODE model, and the results that will be presented in this section are qualitatively similar to those observed in Chapter 3. We then incorporated dispersal into the deterministic model to explore what effect local dispersal can have on species presence-absence. We also varied the strength of dispersal D to examine the effects of local dispersal on the occurrence priority effects in the deterministic model.

For example, Figure 5.2 shows the presence-absence of species at $\alpha = 1.28$ predicted by the deterministic models (5.1) with zero (first row), weak (second row), medium (third row) and strong dispersal (fourth row), with two different initial conditions: initial abundances favour species 3 (left column); and initial abundances favour species 1 and 2 (right column). To understand the dynamical behaviour of equation (5.1) for a range of values of the interspecific competition coefficient α across locations x, we constructed summary plots of the deterministic model using three different initial abundances, each favouring one of the three species. These plots are shown in Figure 5.4 (left column). To do this, we conducted numerical experiments at a grid in (x, α) and coloured different pixels of the summary plots according to which combination of species is present at each location x. Consistent with previous ecological studies

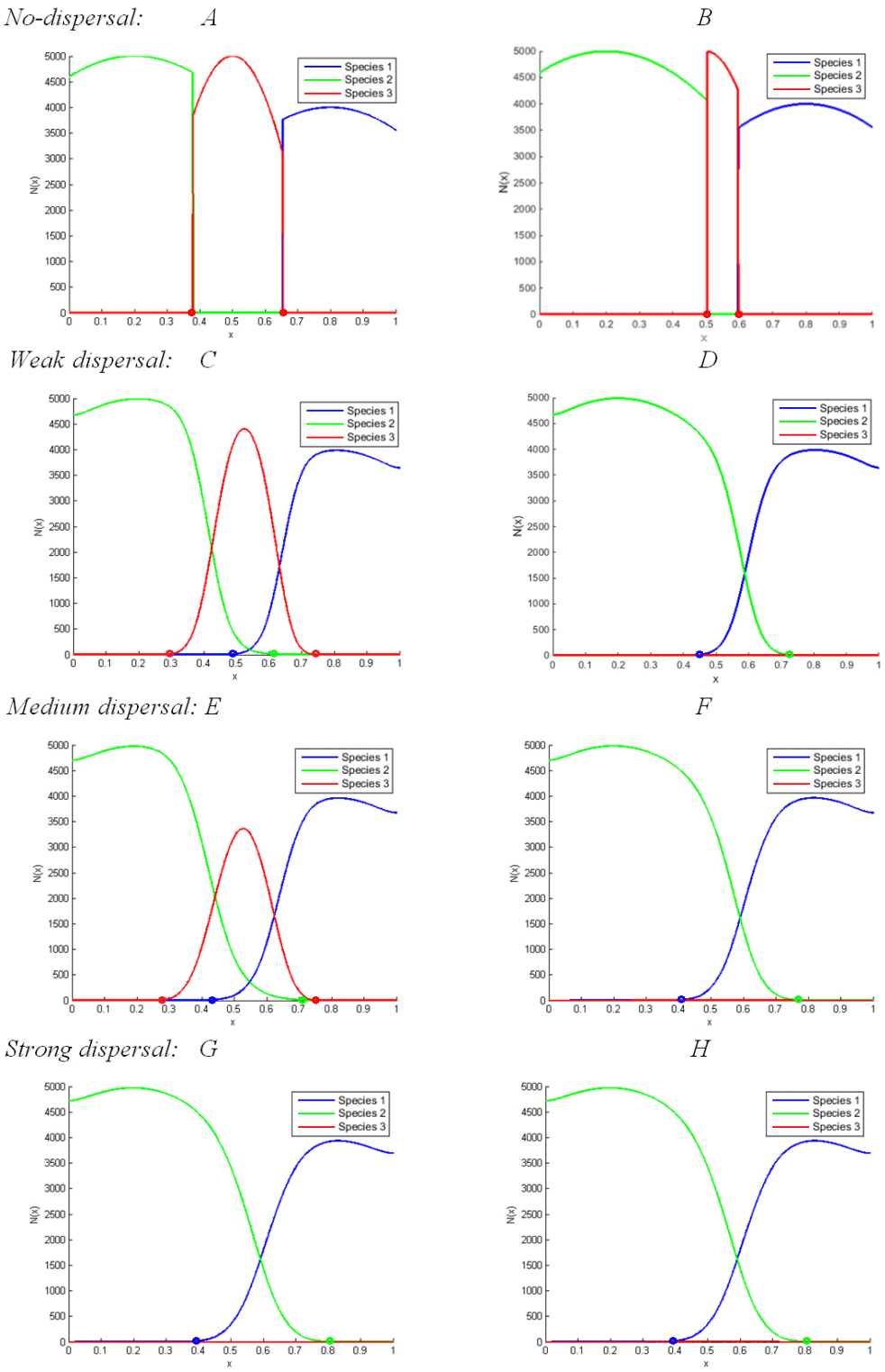


FIGURE 5.2: Results of the deterministic models: $D = 0$ (A,B); $D = 0.0005$ (C,D); $D = 0.001$ (E,F); $D = 0.0015$ (G,H). *Left column*, species densities at $\alpha = 1.28$ when initial abundances favour species 3: $N_1(x) = 0.1K_1(x), N_2(x) = 0.1K_2(x), N_3(x) = 0.9K_3(x)$. *Right column*, species densities at $\alpha = 1.28$ when initial abundances favour species 1 and 2: $N_1(x) = 0.9K_1(x), N_2(x) = 0.9K_2(x), N_3(x) = 0.1K_3(x)$. Circles correspond to the range limits of species. Carrying capacities are as in Figure 5.1. These plots are computed by numerical simulation with MATLAB `pdepe` solver.

[61], [162], [163], we define a species to be present if its density is greater than 0.5% of the maximum density of that species. This can be thought of as a detection threshold (i.e. meaning that we would not observe a species that is present at a sufficiently low density). We have also investigated the outcomes of the models using various ecological criteria (e.g. 0.5% of the maximum carrying capacity of that species, $K_{i,max}$; 0.5% of the maximum density of any species; and 0.5% of the maximum total density of species); the results presented in this section are robust to reasonable choices of presence-absence criterion.

To discuss the effects of local dispersal on priority effects, we first focus on the left-hand column of the summary plots (Figure 5.4A, C, E, G). The right-hand column will be explained in the next section. We quantify the prevalence of priority effects as the range of competitive strength α for which priority effects occur. The descriptions of colour coding and shaded regions in the summary plots are as follows: (i) diagonal shaded indicate single species present with species 1 (*blue*), species 2 (*green*), and species 3 (*red*); (ii) horizontal shaded indicate two-species coexistence with species 2 and 3 (*pink*), species 1 and 3 (*brown*) and species 1 and 2 (*yellow*); (iii) vertical shaded indicates three-species coexistence (*cyan*); (iv) unshaded indicate priority effect regions, where the meaning of these colours are described in a graphical legend in Figure 5.4.

No dispersal. Figure 5.4A depicts the summary plot for the range limits of species predicted by the deterministic model with no dispersal, as the strength of biotic interactions α and location x change. Different colours represent different combinations of species presences. Changes in colour correspond to a range limit of at least one species. As with linear environmental gradient case (Chapter 3), when $\alpha < 1$, coexistence is possible in which two (horizontal-shaded pink, brown and yellow regions) or three (vertical-shaded cyan region) species are present (Figure 5.4A). However, when $\alpha > 1$, there can be alternative stable states. Ecologically, this is known as a priority effect [170]. In this case, the deterministic model shows bistable (dark green and teal regions) and tristable (light grey region) behaviour, with each steady state at its single-species carrying capacity. Which steady state is reached depends on the initial abundances of species. This is illustrated in Figure 5.2A, B, where, due to competitive exclusion, only one species can exist at any given location, but the species range limits depend on

initial abundances.

Weak dispersal. Figure 5.4C illustrates the presence-absence of species in the deterministic model with weak dispersal. A major effect of dispersal is to increase coexistence. When $\alpha < 1$, dispersal causes the zone of two-species (pink, brown and yellow regions) and three-species coexistence (cyan region) to increase compared to no-dispersal case (Figure 5.4A). When $\alpha > 1$, dispersal reduces competitive exclusion (of all but one species) effects that occur in no-dispersal case (Figure 5.2A, B) and promotes coexistence of species (Figure 5.2C, D). Inclusion of weak dispersal into the deterministic model leads to replacement of single-species steady states (dark green, teal and light grey regions in Figure 5.4A) with single- and multiple-species steady states (purple, orange, dark grey, black and white regions in Figure 5.4C). We also observe that the minimum value of the interspecific competition coefficient α required to observe priority effects is larger, in contrast to no-dispersal case (compare unshaded regions in Figure 5.4C with Figure 5.4A)

Medium dispersal. Figure 5.4E demonstrates the presence-absence of species in the case of moderate dispersal levels. When $\alpha < 1$, increasing the strength of migration from weak to medium dispersal causes the zone of three-species coexistence (cyan region) to increase. When $\alpha > 1$, moderate dispersal enhances the occurrence of priority effects: this phenomenon occurs for smaller values of the interspecific competition coefficient α (compare unshaded regions in Figure 5.4E with Figure 5.4C). In general, different combinations of two stable (single- or multiple-species) steady states are observed within each of priority effect regions. For instance, near the centre of the region, there are two stable steady states: three-species coexistence (Figure 5.2E); or two-species coexistence with species 3 absent (Figure 5.2F). Which of these two steady states is reached depends on initial abundances.

Strong Dispersal. When $\alpha > 1$, priority effects occur in the cases of relatively weak and medium dispersal, where coexistence of three-species near the centre of the region is possible. We observe that strong dispersal leads to fewer occurrences of priority effects (compare unshaded regions in Figure 5.4G with Figure 5.4E) and results in extinction of certain species. For instance, in Figure 5.2G,H, species 3 is excluded throughout the entire region.

Based on these findings, dispersal can have different effects on the outcome of species interactions: on one hand, moderate dispersal enhances priority effects and allows dispersal-mediated coexistence; on the other hand, strong dispersal can lead to disappearance of priority effects. Consequently, dispersal-induced extinction phenomenon occurs, with some species (e.g. species 3) being excluded from the entire locations. This occurs due to rapid dispersal of neighbouring competitors into the niche of a focal species.

5.3.2 The Impacts of Stochasticity on the Occurrence of Priority Effects for Large Population

Figure 5.3 shows the average species densities (bar graphs) at $\alpha = 1.28$ predicted by the stochastic IBM for large populations under initial abundances that favour either species 3 (left column) or species 1 and 2 (right column). Averages are calculated over $N = 500$ realisations of the stochastic model. For comparison, the densities of species predicted by the deterministic model are also shown using solid lines. Summary plots of the stochastic model (α against x) are shown in Figure 5.4 (right column). These plots are generated using $N = 100$ realisations for each value of α and for three different initial abundances (i.e. initial abundances favouring each species). When there are priority effects, individual realisations of the IBM with the same initial conditions can converge on different outcomes. We categorised each realisation according to which species were present before averaging species abundances across realisations in the same category. As with the deterministic model, we applied the 0.5% detection threshold to the average abundance data to determine the presence-absence of species across x. The grey pixels in Figure 5.4 indicate small stochastic variations in range boundaries among IBM realisations.

Overall, the results of the IBM with large population sizes agree with those of the deterministic model. Comparisons of deterministic with stochastic models on the range-limit predictions (coloured circles in Figure 5.2 and Figure 5.3, and range boundaries between different coloured regions in Figure 5.4) have indicated agreement between the two models. The main difference between these two models is that, under weak or medium dispersal, priority effects start at lower values of α in the stochastic

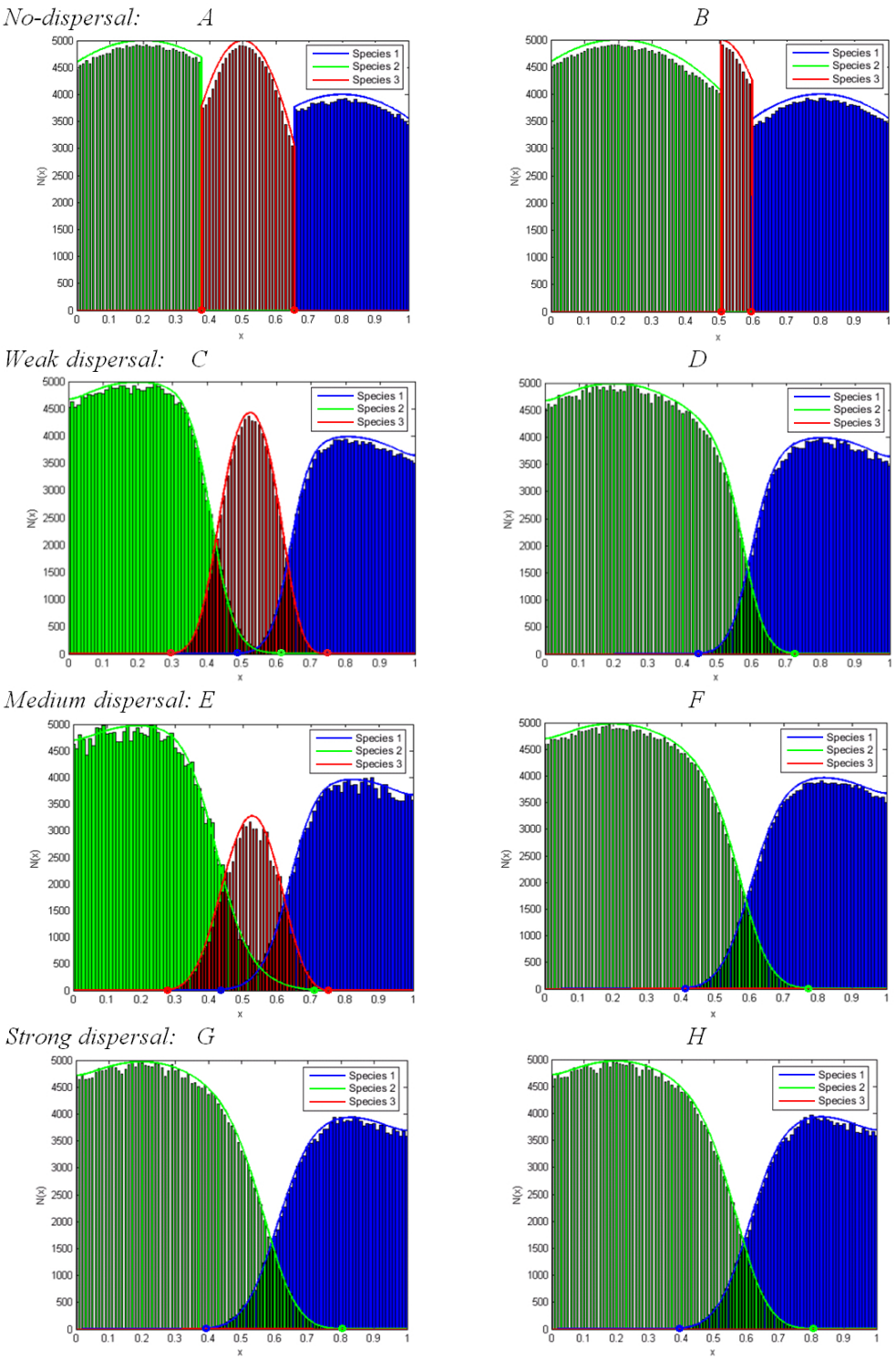


FIGURE 5.3: Results of the stochastic IBM for large populations: $D = 0$ (A,B); $D = 0.0005$ (C,D); $D = 0.001$ (E,F); $D = 0.0015$ (G,H). *Left column*, average species densities at $\alpha = 1.28$ (IBM: bar graphs; deterministic model: solid lines) when initial abundances favour species 3: $N_1(x) = 0.1K_1(x), N_2(x) = 0.1K_2(x), N_3(x) = 0.9K_3(x)$. *Right column*, average species densities at $\alpha = 1.28$ (IBM: bar graphs; deterministic model: solid lines) when initial abundances favour species 1 and 2: $N_1(x) = 0.9K_1(x), N_2(x) = 0.9K_2(x), N_3(x) = 0.1K_3(x)$. Circles correspond to the range limits of species. Carrying capacities are as in Figure 5.1. These plots are computed by MATLAB simulations until time $T = 1000$ and then the realisations are averaged.

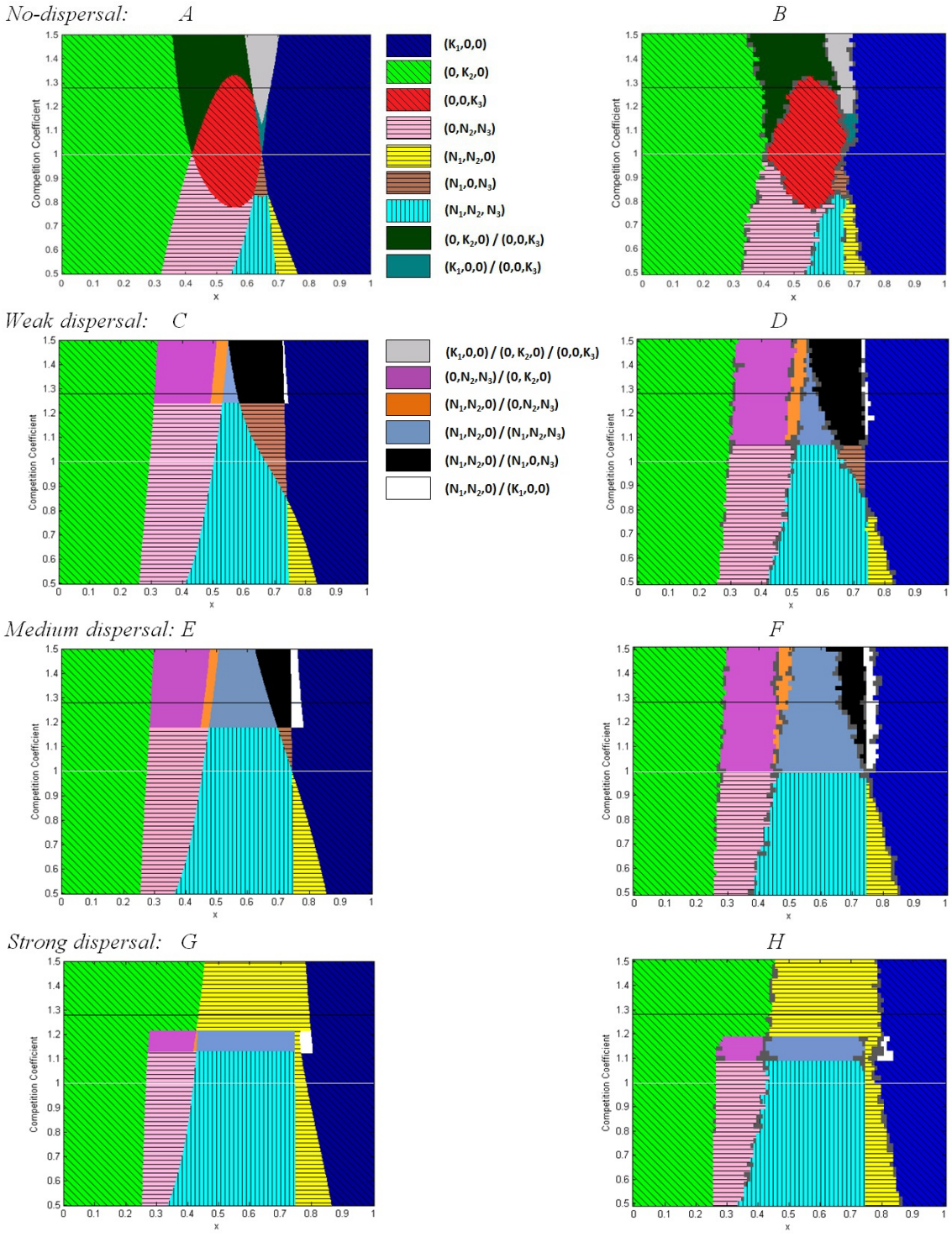


FIGURE 5.4: Results of the deterministic model and stochastic IBM for large populations: $D = 0$ (A,B); $D = 0.0005$ (C,D); $D = 0.001$ (E,F); $D = 0.0015$ (G,H). *Left (respectively, Right) column*, summary plots of the deterministic model (respectively, stochastic IBM). Black lines correspond to the value of $\alpha = 1.28$ shown in Figure 5.2 and Figure 5.3; white lines correspond to the value of $\alpha = 1$. Colours correspond to combinations of species presences and the meaning of these colours are described in a graphical legend. Grey pixels near the boundaries between different colour regions indicate chance variation in stochastic IBM, where the results sometimes vary slightly from one realisation to another simply by random chance. Carrying capacities are as in Figure 5.1.

models than in the deterministic models (compare unshaded regions in Figure 5.4D, F with Figure 5.4C, E). Stochasticity therefore causes priority effects to be more influential.

5.3.3 The Impacts of Stochasticity on the Occurrence of Priority Effects for Small Population

Figure 5.5 shows the average species densities (bar graphs) predicted by the stochastic IBM with the carrying capacities $K_i(x)$ reduced to 10% of the values in Figure 5.3. The left (respectively, centre) column shows the results when initial abundances favour species 3 (respectively, species 1 and 2). The results of the deterministic model are also shown using solid lines for comparison. The right column shows the summary plots of the small-population IBM (α against x). In the absence of dispersal in the stochastic model, sites cannot be repopulated from adjacent sites, so populations are more likely to go extinct when carrying capacities are small [184]. Hence, Figure 5.5 only shows the results with dispersal.

The IBM densities (bar graphs) in the interior of species' ranges are consistently smaller than the deterministic predictions (solid lines). This is because, with small populations, some species become absent at certain sites due to stochastic variation. However, the IBM and deterministic model predict similar densities near the edges of species ranges, and the locations of the range limits (coloured circles) are robust to changes in population size. The main difference between the large-population and small-population IBM is that, with small populations, there are fewer occurrences of priority effects (compare unshaded regions in the right-hand columns of Figure 5.4 and Figure 5.5). For instance, the large-population IBM with medium dispersal shows that either two-species coexistence or three-species coexistence is possible near the centre of the domain (Figure 5.3E, F), whereas three-species coexistence is no longer possible in the small-population IBM (Figure 5.5D, E). Overall, the small-population IBM results show that priority effects are eliminated by weaker values of dispersal when population sizes are small than when they are large.

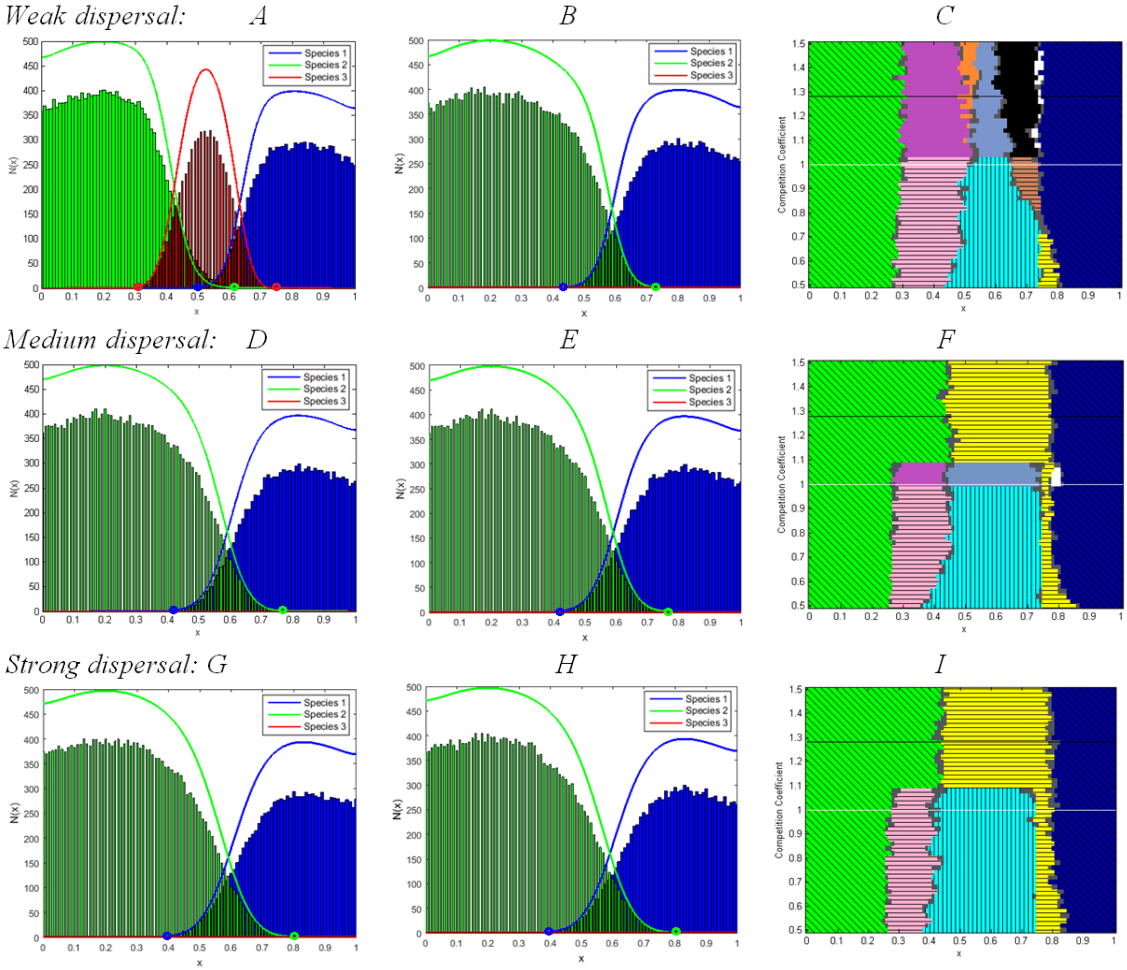


FIGURE 5.5: Results of the stochastic IBM for small populations with $\alpha = 1.28$: $D = 0.0005$ (A,B,C); $D = 0.001$ (D,E,F); $D = 0.0015$ (G,H,I). IBM: bar graphs; deterministic model: solid curves. *Left column*, average species densities when initial abundances favour species 3: $N_1(x) = 0.1K_1(x), N_2(x) = 0.1K_2(x), N_3(x) = 0.9K_3(x)$. *Centre column*, average species densities when initial abundances favour species 1 and 2: $N_1(x) = 0.9K_1(x), N_2(x) = 0.9K_2(x), N_3(x) = 0.1K_3(x)$. *Right column*, summary plots, black lines correspond to the value of $\alpha = 1.28$ shown in left and centre columns, and white lines correspond to the value of $\alpha = 1$. Colours correspond to combinations of species presences and the meaning of these colours are described in a graphical legend in Figure 5.4. Circles correspond to the range limits of species (in left and centre columns). Carrying capacities are as in Figure 5.1.

5.4 Discussion and Ecological Implications

In this work, we have used deterministic and stochastic models to study the combined influences of dispersal and stochasticity on priority effects that can shape the presence-absence of multiple interacting species. Overall, the occurrence of priority effects depends on the magnitude of dispersal and strength of biotic interactions in both models. First, we demonstrate the conditions under which priority effects occur as dispersal intensity changes. We show that moderate dispersal enhances priority effects and permits dispersal-mediated coexistence; stronger dispersal leads to reduction of priority effects and exclusion of some species (Figure 5.4C, E, G). From an ecological viewpoint, these findings have qualitative implications for conservation biology: artificial movement corridors can be constructed to facilitate the migration of declining species from fragmented or degrading habitats [16], [123]. Our results suggest that the risk of dispersal-induced extinction should be considered in the design of such corridors as a conservation tool. This may require accurate knowledge of dispersal rates and biotic interactions, as well as just abiotic variables.

Our observations on the different effects of dispersal on presence-absence of species confirm what previous studies have found [21], [23], [46], [48]. By dispersing to other locations, interacting species have the possibility of finding new populations and expanding their range limits [48]. In an ecological community, dispersal can facilitate coexistence of species by avoiding biotic interactions from other species [9], [48], [70], [122]. However, some studies show that asymmetric dispersal can be detrimental to coexistence and lead to exclusion of species [46], [58], [80]. This different effect of dispersal is also evident in the presence of priority effects [21], [23], [69], [124] and severe asymmetric competition [9], [128] where high dispersal rates can lead to the exclusion of some species throughout all suitable habitats.

Unlike deterministic models, the predictions of priority effects in the stochastic models are sensitive to population size. For large (respectively, small) populations, there are more (respectively, fewer) occurrences of priority effects in the stochastic models than in the deterministic models. This is not just true for the system we considered here; empirical studies [26] illustrate that priority effects are more likely to appear in

systems with large populations and lower migration rates. Our IBM findings support this empirical observation, and in our models, the influence of biotic interactions is also necessary. For large populations, we observe that priority effects occur for smaller values of the interspecific competition coefficient α in the stochastic models (Figure 5.4D, F) than in the deterministic models (Figure 5.4C, E). In this case, while the deterministic model predicts multi-species coexistence is possible, the IBM results demonstrate that fluctuations arising from stochasticity can interfere with species establishment order. Consequently, the neighbouring competitors have the potential to establish themselves first and exclude the focal species in some realisations where deterministic models would predict that the focal species would be present. Differences between predictions of deterministic and stochastic models are also evident in other studies [2], [99]: these studies show that demographic stochasticity can have a strong impact on the dynamics of large populations of species when stabilisation mechanism is very weak (i.e. correspond to the competitive pressure, with $\alpha \geq 1$) and fitness differences are small. In our findings, this situation corresponds to the competitive outcomes near the central region, where the differences in carrying capacity are small. Some studies [188], [195] also suggest that stochastic effects may be enough to push the system towards an alternative community assembly (e.g. extinction of some species).

We also observe that priority effects are eliminated by weaker values of dispersal when population sizes are small (Figure 5.5F) than when they are large (Figure 5.4F). These findings illustrate the reduction of priority effects in small populations because of random extinction events; in small-population IBM, due to lower average densities of species, stochasticity may cause the focal species to go extinct, making it more likely that the smaller community will eventually be dominated by the neighbouring competitors in all realisations. It has also been demonstrated in different studies [2], [99], [185] that species which can coexist with other species in smaller community are more likely to go extinct when stochasticity is incorporated. Small local populations facing extinction can be rescued by migration of individuals from adjacent sites, where the birth and immigration processes of individuals can enhance the likelihood of species persistence [15]; however, rapid dispersal may lead to higher extinction risk of small populations, particularly in sink habitats with emigration rates exceeding immigration

rates [125]. Interacting species at low densities may also experience hardships in mate finding and difficulties in avoiding severe biotic interactions from other species [49], [84]; these situations can affect chance in birth and death rates and consequently reduce the likelihood of persistence. Ecologically, small population sizes are crucial in the study of endangered or invasive species because high-mortality events can be exacerbated by demographic stochasticity [14]. Our work suggests that ecologists should consider the use of stochastic models when predicting the presence-absence of species with small populations. This is because stochasticity strongly influences the dynamics of small populations, which can induce an uncertainty in the predictions of species presence-absence. By improving estimates of potential presence-absence of species, wasted surveillance effort and huge mitigation cost for conservation programs [79] may be avoided.

In conclusion, this study adds to our understanding of the strengths and weaknesses of different modelling approaches, and the possible implications on the predictions of species presence-absence. We recommend the use of both stochastic and deterministic models to predict the joint effects of dispersal, environment and biotic interactions on the presence-absence of species when the local populations are large. However, we suggest that the range of possible outcomes will be revealed better by stochastic models when the populations are small.

Chapter 6

Non-Local Dispersal

6.1 Introduction

In this chapter, we address the following questions:

- Are ecological communities with non-local dispersal (i.e. dispersal process that occurs over non-adjacent or larger spatial locations) more likely to exhibit priority effects than localised dispersal?
- How does non-local dispersal affect species coexistence and the occurrence of priority effects as dispersal distance changes?

Answering these questions require better understanding of species dispersal mechanisms [55], [96], [103], [181] and considering the roles of biotic interactions [23], [67], [69], [199] and abiotic environments [112], [157], [169], [173]. In the previous chapter (Chapter 5), we observed contrasting effects of local dispersal on the occurrence of priority effects that can shape presence-absence of multi-species communities. In the case of strong dispersal, priority effects vanish; consequently, rapid dispersal causes extinction of some species. In contrast, for moderate dispersal levels, priority effects persist, which has the effect of promoting coexistence at the same locations. Other studies have also demonstrated that priority effects and ecological processes such as local dispersal can be important drivers of community assembly over small spatial scales [21], [23], [124], but the persistence of this phenomenon under non-local dispersal process has yet to be addressed. At present it remains unclear whether the effects of non-local dispersal can lead to the persistence or exclusion of priority effects across heterogeneous environments with biotic interactions among multiple species.

In this chapter, we fill part of this knowledge gap by exploring the possible occurrence of priority effects in community assembly using various models of dispersal. This investigation is inspired by the dispersal biology of species: for example, some plant seeds are often dispersed over short distances and near to their parents' locations [20], [147]. Consistent with this observation, theoretical models are developed with the assumptions that species can move locally between adjacent sites while interacting with other species. These assumptions serve as a basis of several modelling frameworks with local dispersal process such as PDE models [21], [23], [46] (as in Chapter 4) and stochastic (random walk) models [29] (as in Chapter 5). However, there are some plant seeds that being transported longer distances by dispersal vectors such as animals, wind and water [20], [86], [98], [147], [148]. Some animal species also show a non-local dispersal pattern [56], [153]: for instance, Drobzhansky and Wright [45] discover that the spatial dispersal distribution of fruit flies illustrates a long-distance dispersal movement. This observation on non-local dispersal pattern between fruit fly species is also evident in other studies [49], [117]; for instance, Etienne et al. [49] show how the incorporation of non-local dispersal processes using a dispersal kernel (i.e. the distribution function that describes the probability of dispersal to different locations) into a modelling framework can affect the predicted population dynamics of species. They find that the establishment and persistence of species are determined by the modes of dispersal, where non-local dispersal can further enhance the chance of species survival [49]. Conversely, some experimental studies discover that species richness is rapidly lost when ecological processes such as dispersal occur over relatively large spatial scales [114], whereas coexistence of species are possible when ecological processes are localized [114], [160]. Given these contrasting observations on non-local dispersal, its effects on community assembly is not well understood in the presence of priority effects, which are mediated by intense biotic interactions.

To explore how the establishment order of species interacts with non-local dispersal to shape multi-species communities, we extend previous deterministic theoretical

studies consisting of biotic interactions and environmental gradients [133], [164] to incorporate a dispersal kernel into the models; this inclusion leads to a system of integro-differential equations (IDE). We examine the consequences of different dispersal mechanisms on community dynamics by comparing simulation results of non-local dispersal (IDE) with local dispersal (PDE) models under varying dispersal intensity. We discover that these two models can give qualitatively similar or different predictions of priority effects, depending on dispersal distance and its magnitude. In the case of short-range dispersal, we observe the agreement between IDE and PDE predictions for weak and medium dispersal strength, but disagreement for relatively strong dispersal scenario. Computations using numerical continuation methods reveal the bifurcations controlling the behaviour of the two models when parameters are varied; in particular, we illustrate the existence of a threshold value in dispersal strength (i.e. saddle-node bifurcation) above which priority effects disappear. Our two-parameter continuation result reveals that there is a co-dimension 2 point, corresponding to a degenerate transcritical bifurcation: at this point, the transcritical bifurcation changes from subcritical to supercritical with corresponding creation of a saddle-node bifurcation curve. Furthermore, we observe contrasting effects of non-local dispersal as dispersal distance changes: while very long-range dispersal can lead to species extinctions, intermediate-range dispersal can permit more outcomes where multi-species coexistence is possible than short-range dispersal (or purely local dispersal). Overall, both continuation and simulation results show that priority effects are more pronounced in the non-local dispersal models than in the local dispersal models. As explained in Chapter 1, priority effects are a strong factor in determining the presence-absence of multiple species. Taken together, our findings highlight the profound impact of non-local dispersal process: "big steps" in this case have more influence than many "small steps" in mediating priority effects.

6.2 A Deterministic Model with Biotic Interactions and Non-Local Dispersal

We model a non-local dispersal process across heterogeneous environments where biotic interactions among multiple species are present. The occurrence of non-local dispersal events is encoded via a dispersal kernel. To this end, we consider a system of integro-differential equations (IDE) for the densities $N_i\,(x,\ t)$ of m species in a one-dimensional domain $a_L \leq x \leq a_R$:

$$\frac{\partial N_i}{\partial t} = \frac{r_i N_i}{K_i(x)}\left(K_i(x) - \sum_{j=1}^{m} \alpha_{ij} N_j\right) + \rho_i\left[\int k(x-y)N_i(y)dy - N_i(x)\right] \qquad (i = 1, 2, ..., m) \tag{6.1}$$

where r_i is the intrinsic growth rate, α_{ij} is the coefficient for competition of species j on species i, K_i is the carrying capacity, ρ_i is the the dispersal rate of non-local dispersal process and $k(x-y)$ is the probability density function of species moving from location y to x. The function $k(x-y)$ is called the dispersal kernel, in which we assume that the kernel is a non-negative, symmetric and of unit mass. As usual, by rescaling the density of species i relative to its intraspecific competition coefficient α_{ii}, we may effectively set the intraspecific competition coefficients α_{ii} to equal 1, and the remaining competition coefficients α_{ij} represent the ratio of intraspecific to interspecific competition. Equation (6.1) is a spatially extended Lotka-Volterra competition model [23], [69], [164], which becomes an IDE with the addition of the non-local dispersal kernel.

The dispersal kernel models movement of species to non-adjacent spatial locations, with the parameter ρ_i representing the strength of non-local dispersal for species i. We employ an exponential dispersal kernel similar to [101], [109] as an example, in order to illustrate the effects of non-local dispersal in a multi-species community dynamics:

$$k(x) = \begin{cases} c_b\, e^{\frac{b^2}{x^2-b^2}} & , |x| < b \\ 0 & , otherwise \end{cases} \tag{6.2}$$

TABLE 6.1: Parameter values.

Symbol	Description	Parameter Values
r_i	The intrinsic growth rate of species i	1
$K_{1,max}$	As indicated in equation (5.2)	3500
$K_{2,max}$	As indicated in equation (5.2)	5000
$K_{3,max}$	As indicated in equation (5.2)	5000
x_1	As indicated in equation (5.2)	0.8
x_2	As indicated in equation (5.2)	0.2
x_3	As indicated in equation (5.2)	0.5
w_1	As indicated in equation (5.2)	0.6
w_2	As indicated in equation (5.2)	0.7
w_3	As indicated in equation (5.2)	0.25
D_i	Diffusion coefficient	0-0.0025
b	Dispersal distance	0.25
ρ_i	Dispersal strength in IDE (calculated using equation (6.3))	
α_{ij}	Competition coefficient (values given in figure captions)	

where b characterises dispersal distance and c_b is a normalisation constant such that $\int k(x)dx = 1$. Other types of function for the non-local dispersal could also be chosen [28], but we chose the dispersal kernel given by (6.2) primarily because of the convenient interpretation of the distance parameter, b, in the exponent. Since symmetric kernel is employed, this indicates that odd moments such as mean equal 0, and kernel shape is summarised by even moment such as mean-squared displacement. To fairly compare the non-local dispersal models (6.1) and local dispersal models, we imposed the condition that their mean-squared displacements (per unit time) are equal. Note that the mean-squared displacement for the diffusion model is $2D_i$, while the mean-squared displacement for the dispersal kernel, $\rho_i\sigma^2$, is calculated numerically (i.e. by using second moment with $\sigma^2 = \int x^2 k(x)dx$). The relationship between the dispersal rate ρ_i of the IDE model with the diffusion coefficient D_i of the PDE model [89], [131], [145], [176] is given by:

$$\rho_i = \frac{2D_i}{\sigma^2} \tag{6.3}$$

6.2.1 Numerical Methods

Equation (6.1) is solved numerically using the method of lines as follows. The method of lines involved a discretisation of spatial domain $a_L \leq x \leq a_R$ into a mesh with $A+1$ equally spaced nodes $x_j = a_L + jh$ for $j = 0, 1, ..., A$, where $h = \frac{a_R - a_L}{A}$ is the uniform mesh size. The integral term in (6.1) is approximated by trapezoidal rule with the same discretisation. This leads to a system of $3(A+1)$ ODE, one for the density of each species at a series of equally spaced x points. The resulting system of ODE is solved by a standard ODE solver, `ode15s` for $t = 1000$. We used $h = 10^{-2}$ and initial conditions as indicated in each figure section. The results are insensitive to a reduction in grid spacing h.

We also verified that steady state is stable. As usual, the time derivative in equation (6.1) is set to zero. We then discretised equation (6.1) by introducing a mesh with $A+1$ equally spaced nodes $x_j = a_L + jh$ for $j = 0, 1, ..., A$, where $h = \frac{a_R - a_L}{A}$ is the uniform mesh size. The integral term in (6.1) is approximated by trapezoidal rule with the same discretisation. This yields a system of $3(A+1)$ non-linear equations, one for the density of each species at a series of uniformly spaced x points. This system is solved for steady state using MATLAB `fsolve` with initial guess is the same as initial condition indicated in each figure section. To determine the stability of steady state, the Jacobian matrix is calculated numerically in `fsolve` and then the eigenvalues are computed using `eig` function. The steady state is stable if all eigenvalues have negative real parts.

We also used numerical continuation package XPPAUT to check our simulation results. Equation (6.1) is discretised using the method of lines with the integral term is approximated by sums using `conv` operator. This yields a system of ODE, which is solved for steady state in XPP using `cvode` solver for $t = 1000$. Then, the steady state is continued in AUTO, in which we tracked stable and unstable steady states, and also bifurcation points as a model parameter changes. Continuation results shown in this chapter used a maximum/minimum allowable step size of parameter, $10^{-1}/10^{-6}$. Unless otherwise stated, parameter values used in the simulation are given in Table (6.1).

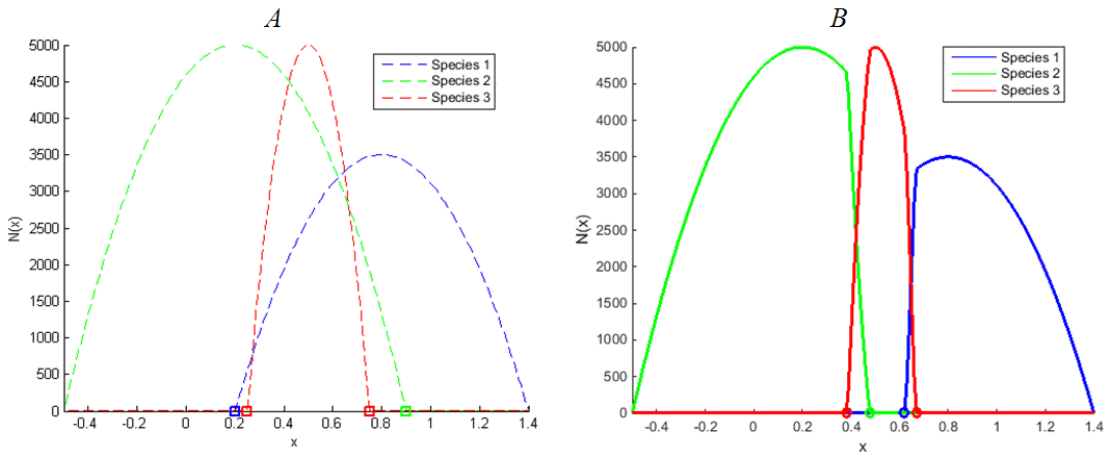


FIGURE 6.1: *A*, The nonlinear carrying capacities (dotted lines) following equation (5.2) for species 1 (blue), species 2 (green) and species 3 (red) with squares representing the range limits of species in the absence of biotic interactions. *B*, Modelling results with no-dispersal ($D_i = \rho_i = 0$) with circles representing the range limits of species in the presence of biotic interactions. Competition coefficient: $\alpha_{ij} = 0.85$. Other parameter values as in (6.1).

6.3 Results

In the absence of dispersal ($p_i = D_i = 0$), we have shown in Chapter 3 that the presence-absence of species depend on the strength of biotic interactions. When $\alpha < 1$ (i.e. interspecific competition is weaker than intraspecific), species can coexist at the same location; for instance, Figure 6.1B shows modelling results with no dispersal when $\alpha < 1$, with coexistence of species are possible near the central region. Competition from species 2 (green) and species 3 (red) eliminates species 1 (blue) from some locations x and shifts the range limit of species 1 from $x = 0.2$ (blue square, Figure 6.1A) to the right (blue circle, Figure 6.1B); similarly, the range limits of species 2 (green circle) and species 3 (red circles) are affected due to biotic interactions.

When $\alpha > 1$ (i.e. interspecific competition is stronger than intraspecific), priority effects occur with the range limits of species depend on initial abundances and also the strength of dispersal (i.e. when $p_i, D_i > 0$). In the following sections, we demonstrate the effects of different modes of dispersal on the presence-absence of species, and we highlight the similarities and differences between the simulation results from non-local and local dispersal models, with respect to the occurrence of priority effects and species coexistence.

6.3.1 The Effects of Different Modes of Dispersal on Priority Effects in the Case of Short-Range Dispersal

When dispersal is incorporated into the models ($p_i, D_i > 0$), the presence-absence of species is influenced by movement of individuals from other locations. For example, Figure 6.2 shows the range limits of species predicted by the local dispersal (PDE) model, which are similar results to those observed in Chapter 5. In this chapter, we extend the spatial domain x to be larger (as compared to Chapter 5) to eliminate the boundary effects so that both models can be fairly compared. Figure 6.2 depicts species presence-absence at $\alpha = 1.28$ for zero (first row), weak (second row), medium (third row), strong (fourth row) and stronger (fifth row) dispersal levels, with two different initial conditions: initial abundances favour species 3 (left column); and initial abundances favour species 1 and 2 (centre column). The right column shows summary plots of the PDE model for a range of values of the interspecific competition coefficient α. These plots depict which combination of species is present at a each location x and are generated using three different initial abundances i.e. initial abundances favour each species. As in Chapter 5, we define a species to be present if its density is greater than 0.5% of the maximum observed density of that species. This can be thought of as a detection threshold (i.e. meaning that we would not observe a species that is present at a sufficiently low density). To illustrate the effects of non-local dispersal on the presence-absence of species, we constructed Figure 6.3 using IDE model (6.1) with short-range dispersal (e.g. $b = 0.25$), which has similar layout and comparable to the local dispersal results (Figure 6.2).

In general, the results of the IDE are in agreement with those of the PDE, particularly for weak and medium dispersal levels: when $\alpha > 1$, we observe priority effects that depend on initial abundances in both models. As discussed in Chapter 3, without dispersal ($p_i = D_i = 0$), coexistence of species is impossible, in which only one species can exist at any given location x through priority effects (Figure 6.2A, B, C and Figure 6.3A, B, C). Increasing the intensity of dispersal from weak to medium dispersal levels enhances the occurrence of priority effects (compare unshaded regions in Figure 6.2F, I and Figure 6.3F, I). This situation promotes coexistence of two (Figure 6.3E, H and Figure 6.2E, H) or three species (Figure 6.3D, G and Figure 6.2D, G) near the

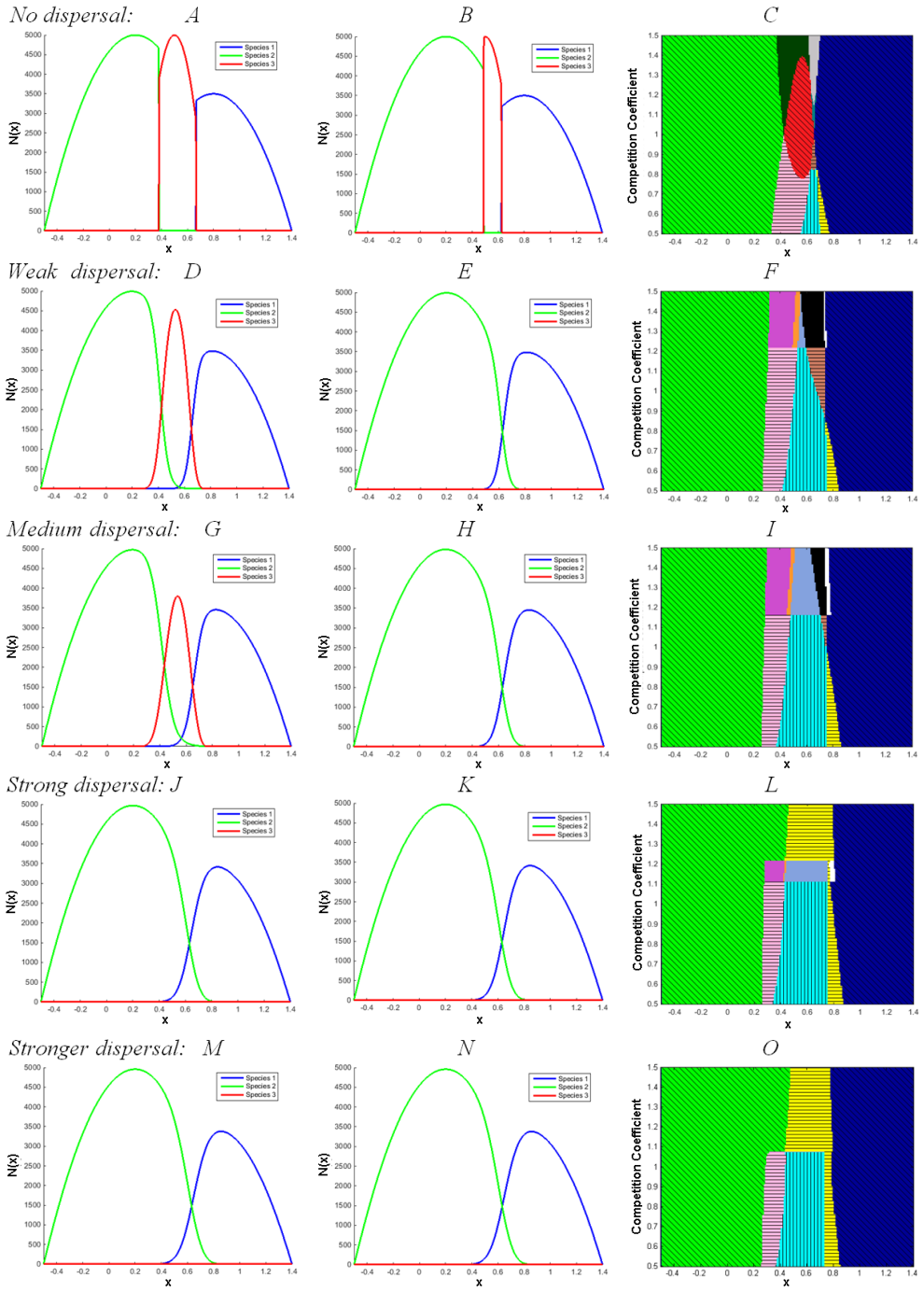


FIGURE 6.2: Results of the PDE model under various dispersal scenarios: $D = 0$ (A,B,C); $D = 0.0005$ (D,E,F); $D = 0.001$ (G,H,I); $D = 0.0015$ (J,K,L); $D = 0.002$ (M,N,O). *Left column*, species densities at $\alpha = 1.28$ when initial abundances favour species 3: $N_1(x) = 0.1K_1(x), N_2(x) = 0.1K_2(x), N_3(x) = 0.9K_3(x)$). *Centre column*, species densities at $\alpha = 1.28$ when initial abundances favour species 1 and 2: $N_1(x) = 0.9K_1(x), N_2(x) = 0.9K_2(x), N_3(x) = 0.1K_3(x)$. *Right column*, summary plots, α vs. x (the black lines correspond to the value of α shown in the left and centre columns). Colours correspond to combinations of species present: (i) diagonal shaded correspond to single species presence with: *blue*, $(K_1, 0, 0)$; *green*, $(0, K_2, 0)$; and *red*, $(0, 0, K_3)$; (ii) horizontal shaded correspond to two-species coexistence with: *pink*, $(0, N_2, N_3)$; *brown*, $(N_1, 0, N_3)$; and *yellow*, $(N_1, N_2, 0)$; (iii) vertical shaded corresponds to three-species coexistence with: *cyan*, (N_1, N_2, N_3); (iv) unshaded correspond to priority effect regions, where in (C) *dark green*, $(0, K_2, 0)$ or $(0, 0, K_3)$; *teal*, $(K_1, 0, 0)$ or $(0, 0, K_3)$; *light grey*, $(K_1, 0, 0)$ or $(0, K_2, 0)$ or $(0, 0, K_3)$; (F,I,L,O) *purple*, $(0, N_2, N_3)$ or $(0, K_2, 0)$; *orange*, $(N_1, N_2, 0)$ or $(0, N_2, N_3)$; *grey blue*, $(N_1, N_2, 0)$ or (N_1, N_2, N_3); *black*, $(N_1, N_2, 0)$ or $(N_1, 0, N_3)$; *white*, $(N_1, N_2, 0)$ or $(K_1, 0, 0)$. Carrying capacities are as in Figure 6.1. These plots are computed by numerical simulation with MATLAB `ode15s` solver.

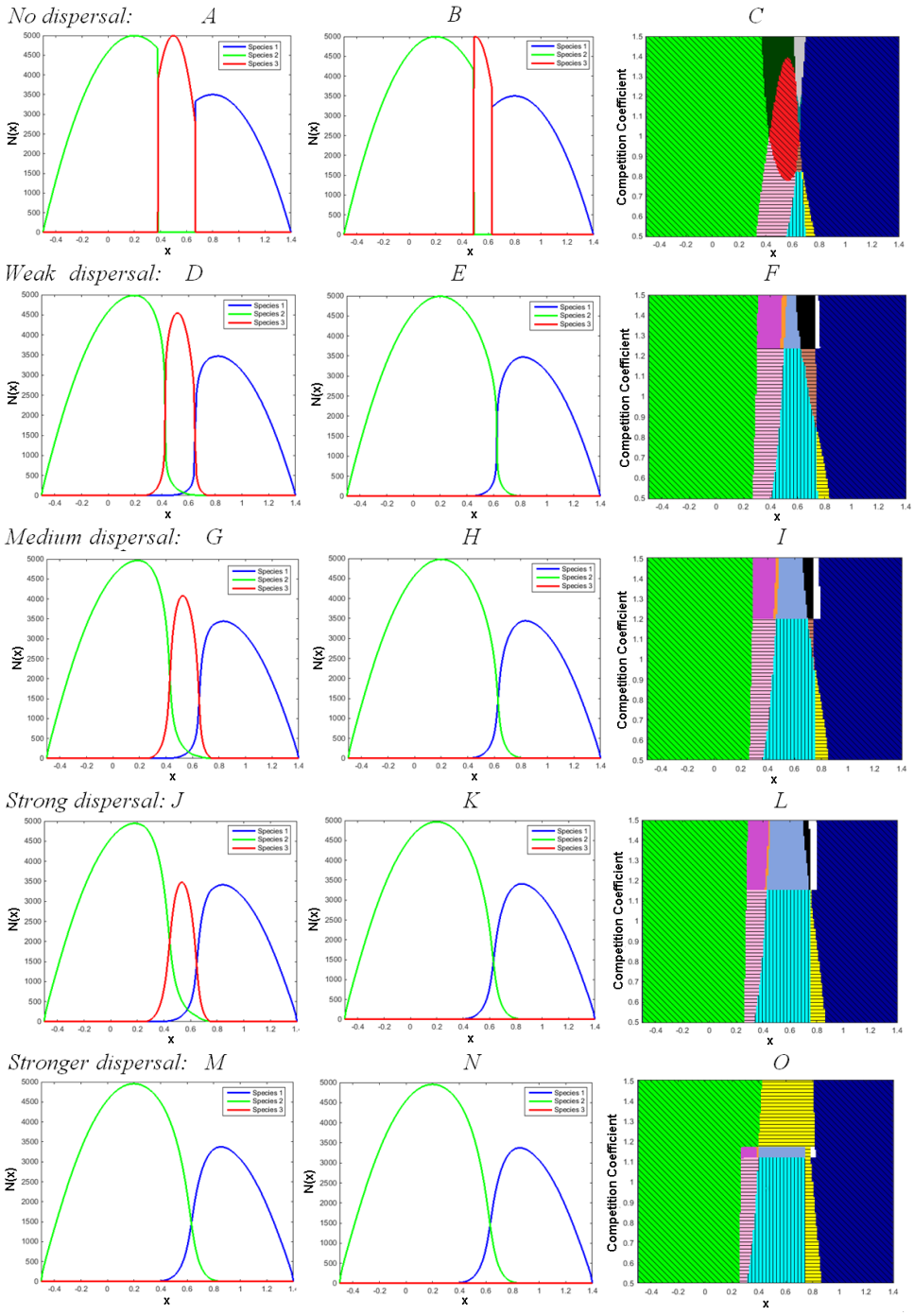


FIGURE 6.3: Results of the IDE model under various dispersal scenarios: $D = 0$ (A,B,C); $D = 0.0005$ (D,E,F); $D = 0.001$ (G,H,I); $D = 0.0015$ (J,K,L); $D = 0.002$ (M,N,O). *Left column*, species densities at $\alpha = 1.28$ when initial abundances favour species 3: $N_1(x) = 0.1K_1(x), N_2(x) = 0.1K_2(x), N_3(x) = 0.9K_3(x)$). *Centre column*, species densities at $\alpha = 1.28$ when initial abundances favour species 1 and 2: $N_1(x) = 0.9K_1(x), N_2(x) = 0.9K_2(x), N_3(x) = 0.1K_3(x)$. *Right column*, summary plots, α vs. x (the black lines correspond to the value of α shown in the left and centre columns). Colours correspond to combinations of species present: (i) diagonal shaded correspond to single species presence with: *blue*, $(K_1, 0, 0)$; *green*, $(0, K_2, 0)$; and *red*, $(0, 0, K_3)$; (ii) horizontal shaded correspond to two-species coexistence with: *pink*, $(0, N_2, N_3)$; *brown*, $(N_1, 0, N_3)$; and *yellow*, $(N_1, N_2, 0)$; (iii) vertical shaded corresponds to three-species coexistence with: *cyan*, (N_1, N_2, N_3); (iv) unshaded correspond to priority effect regions, where in (C) *dark green*, $(0, K_2, 0)$ or $(0, 0, K_3)$; *teal*, $(K_1, 0, 0)$ or $(0, 0, K_3)$; *light grey*, $(K_1, 0, 0)$ or $(0, K_2, 0)$ or $(0, 0, K_3)$; (F,I,L,O) *purple*, $(0, N_2, N_3)$ or $(0, K_2, 0)$; *orange*, $(N_1, N_2, 0)$ or $(0, N_2, N_3)$; *grey blue*, $(N_1, N_2, 0)$ or (N_1, N_2, N_3); *black*, $(N_1, N_2, 0)$ or $(N_1, 0, N_3)$; *white*, $(N_1, N_2, 0)$ or $(K_1, 0, 0)$. Carrying capacities are as in Figure 6.1. These plots are computed by numerical simulation with MATLAB `ode15s` solver.

centre of the region. The main difference between these two models is observed under strong dispersal: there are more occurrences of priority effects in the IDE than in the PDE models (compare unshaded regions in Figure 6.3L and Figure 6.2L). For instance, in unshaded grey blue region near the centre (Figure 6.3L), the IDE models show that either two-species or three-species coexistence is possible (Figure 6.3J, K); however, three-species coexistence is no longer possible in the PDE model (Figure 6.2J, K) with unshaded grey blue region reduces under rapid dispersal scenario(Figure 6.2L). Overall, these results show that priority effects persist when dispersal are strong in the non-local dispersal models, and they are eliminated by stronger values of dispersal in the IDE than the PDE models.

6.3.2 Theoretical Explanations of the (Dis-)Appearance of Priority Effects in the Non-Local and Local Dispersal

To verify the persistence or exclusion of the priority effect in certain regions for both models (Figure 6.2L, O and Figure 6.3L, O), we employed numerical continuation to track the steady states of the models as dispersal strength D changes. Figure 6.4 shows the steady-state density of species 3 at $x = 0.5$ for PDE (thick lines) and IDE (thin lines) models when $\alpha = 1.28$ as dispersal intensity D is varied. There are three branches of steady states: the upper (three-species coexistence) and lower branches (species 3 absent) of steady states are stable (blue curves); these are separated by an unstable steady state (red curve). There is a threshold dispersal strength D_T (respectively P_T) for PDE (respectively IDE), corresponding to a saddle-node bifurcation, beyond which the three-species coexistence state vanishes and priority effects disappear; for values of dispersal $D < D_T$ (respectively $D < P_T$), the density N_3 tends toward upper or lower steady-state, depending on initial species abundances; for values of dispersal $D > D_T$ (respectively $D > P_T$), the priority effects disappear and there is only one stable steady state, in which species 3 is absent. The main difference between the two bifurcation curves in Figure 6.4 is that the saddle-node bifurcation point for the IDE (i.e. P_T) is shifted to stronger dispersal levels at this location, as compared to the PDE model (i.e. D_T).

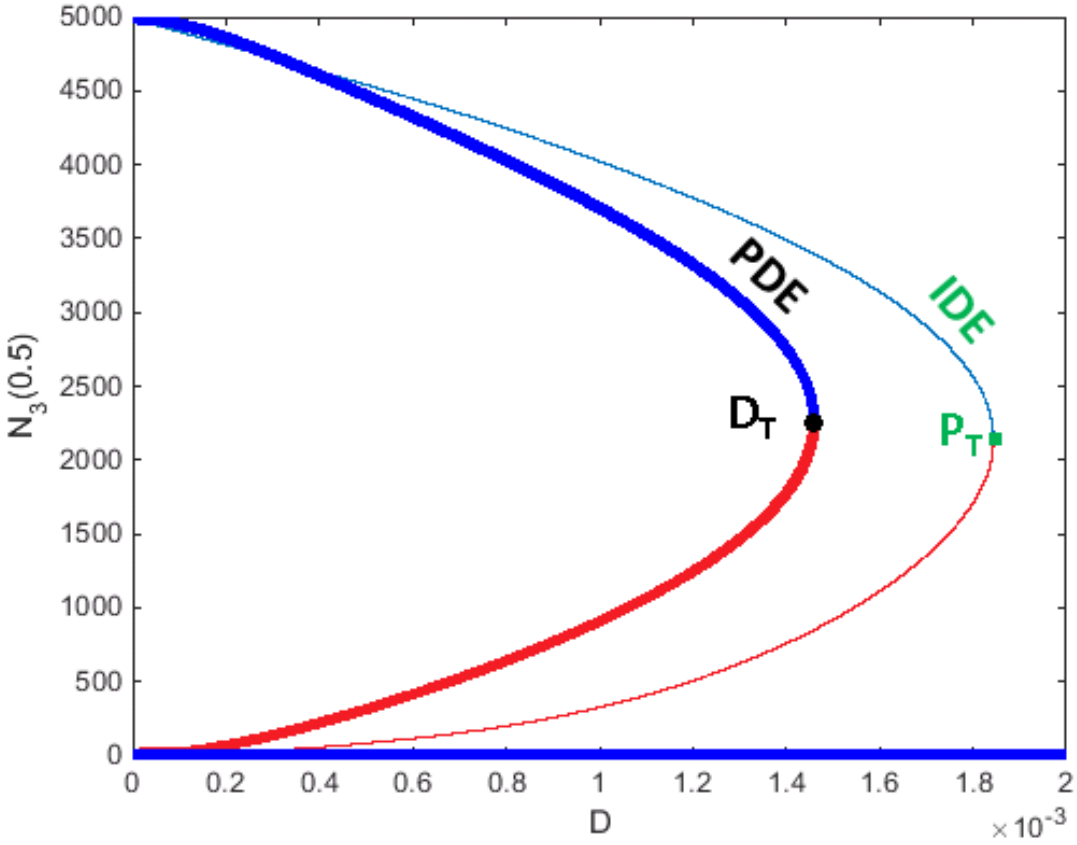


FIGURE 6.4: The density of a focal species (species 3) at $x = 0.5$ and $\alpha = 1.28$ for PDE (thick lines) and IDE (thin line) models as the dispersal strength D change. The threshold values D_T (black point) and P_T (green point) correspond to saddle-node bifurcation points for PDE and IDE, respectively. There are three branches of N_3: (i) unstable three-species steady-states (red curves); (ii) stable three-species steady-state, with species 3 presence (upper blue curves); (iii) stable two-species steady-state, with species 3 absence (lower blue curves). Other parameter values as in Table (6.1). These plots are computed by numerical continuation using XPPAUT.

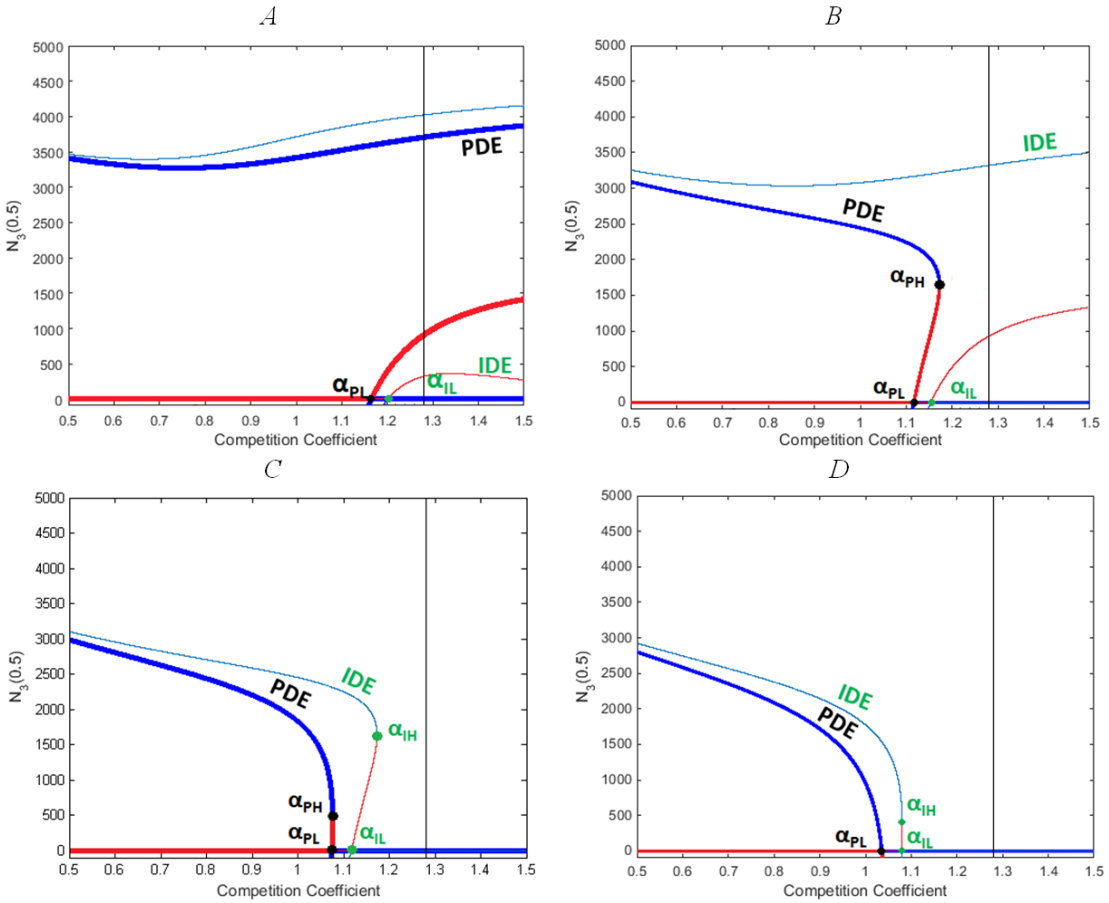


FIGURE 6.5: The density of species 3 (N_3) for PDE (thick lines) and IDE (thin line) models at $x = 0.5$ as the strength of biotic interactions α change under various dispersal scenarios: (A) $D = 0.001$, (B) $D = 0.0015$, (C) $D = 0.002$, (D) $D = 0.0025$. The points α_{PL} and α_{IL} correspond to transcritical bifurcations and α_{PH} and α_{IH} correspond to saddle-node bifurcation points in the PDE and the IDE, respectively. Three branches of N_3: (i) unstable three-species steady-states (red curves); (ii) stable three-species steady-state, with species 3 presence (upper blue curves); (iii) stable two-species steady-state, with species 3 absence (lower blue curves). The black lines correspond to the value of competition coefficient $\alpha = 1.28$ shown by the simulation results in Figure 6.2(PDE) and Figure 6.3 (IDE). Other parameter values as in Table (6.1). These plots are computed by numerical continuation using XPPAUT.

The steady states of the systems are also tracked as the strength of competition α changes under different dispersal scenarios (Figure 6.5) in order to gain better understanding of the dynamics of PDE and IDE simulation results (Figure 6.2 and Figure 6.3). For moderate dispersal levels, as α increases from 0.5 to 1.5 near the central location, our summary plots (unshaded regions of right-hand columns of Figure 6.2F, I and Figure 6.3F, I) show that there is a threshold value for competitive strength, beyond which priority effects appear. Continuation results in Figure 6.5A are consistent with the aforementioned simulation results. Figure 6.5A depicts the steady-state density of species 3 at $x = 0.5$ for the PDE (thick lines) and the IDE (thin lines) models as α changes under medium dispersal. There is a threshold competitive strength α_{PL} (respectively α_{IL}) for the PDE (respectively IDE) models, corresponding to a transcritical bifurcation, beyond which priority effects occur; for competitive strength $\alpha > \alpha_{PL}$ (respectively $\alpha > \alpha_{IL}$), the density N_3 tends toward upper or lower steady-state (blue curves), depending on initial species abundances; for values of competitive strength $\alpha < \alpha_{PL}$ (respectively $\alpha < \alpha_{IL}$), the priority effects vanish and there is only one stable steady state, in which species 3 is present in three-species coexistence. We notice that the threshold value of competitive strength is higher in the IDE (i.e. α_{IL}) than in the PDE (i.e. α_{PL}) models under moderate dispersal levels.

We also observe qualitatively different dynamics between the PDE and IDE models in our summary plots for strong dispersal (unshaded regions of right-hand columns of Figure 6.2L and Figure 6.3L). In particular, there are critical values for competitive strength in which priority effects appear and then vanish in some regions of the PDE summary plot as α increases (Figure 6.2L). Our continuation result (Figure 6.5B: thick curves) reveals that there are threshold values of α (black points) in the PDE models: the lower (respectively, upper) threshold α_{PL} (respectively, α_{PH}) corresponds to transcritical (respectively, saddle-node) bifurcation and priority effects occur for small range of competitive strength i.e. when $\alpha_{PL} < \alpha < \alpha_{PH}$. In the IDE models, for the range of competition coefficient α that we investigated, there occurs a threshold competitive strength α_{IL}, corresponding to a transcritical bifurcation, beyond which priority effects occur; in this situation, priority effects persist for a bigger range of competitive strength α (i.e. when $\alpha > \alpha_{IL}$), which is consistent with the IDE simulation results (Figure 6.3L).

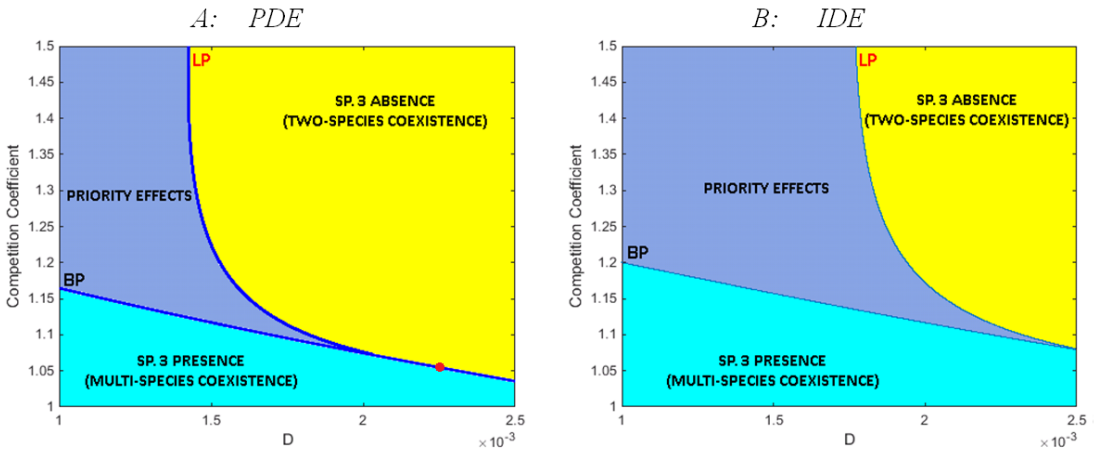


FIGURE 6.6: Parameter space diagram, which summarises different dynamics at location $x = 0.5$ for the PDE (left) and IDE (right) models, as dispersal strength D and competitive strength α are varied. Colours correspond to combinations of species presences: (i) three-species coexistence (cyan); (ii) two-species coexistence with species 3 absence (yellow); (iii) priority effect regions (grey). LP curves correspond to saddle-nodes bifurcations and BP curves correspond to transcritical bifurcations. Points of intersection between BP and LP curves correspond to degenerate transcritical bifurcation point (red point). These co-dimension two bifurcation plots are computed by varying two parameters using numerical continuation package XPPAUT.

As dispersal intensity increases to stronger dispersal, we notice that the priority effects region shrinks in the summary plots of both models (unshaded regions of right-hand columns of Figure 6.2O and Figure 6.3O). Closer investigation of PDE (respectively, IDE) continuation results in Figure 6.5C, D demonstrates that the two bifurcation points, namely transcritical bifurcation α_{PL} (respectively, α_{IL}) and saddle-node bifurcation α_{PH} (respectively, α_{IH}), come closer and closer to one another and, finally, coalesce (compare black (bifurcation) points in Figure 6.5C with Figure 6.5D). To investigate the interaction of transcritical and saddle-node bifurcations and to clarify the disappearance of priority as dispersal strength D and competition coefficient α change, we constructed two-parameter bifurcation diagrams, as shown in Figure 6.6. These plots illustrate the dynamics at the central region $x = 0.5$ as the strength of competition α and magnitude of dispersal D are varied in both models. There is a co-dimension 2 point (red point) for PDE (Figure 6.6A), corresponding to a degenerate transcritical bifurcation: at this point, the transcritical bifurcation (BP) changes from subcritical to supercritical with corresponding creation of a saddle-node bifurcation curve (LP). This co-dimension 2 bifurcation acts as an organising centre and separates the parameter space into three different regions: inside the wedge there are priority effects (grey

colour) with two stable steady states (i.e. three-species coexistence with species 3 presence or two-species coexistence with species 3 absence), and outside the wedge there is one stable steady state (i.e. three-species coexistence with species 3 presence (cyan colour) and two-species coexistence with species 3 absence (yellow colour)). Similar observations are possible in the IDE (Figure 6.6B) as competitive strength α and dispersal intensity D changes (i.e. degenerate transcritical bifurcation occurs when dispersal strength D increases further than the values shown in Figure 6.6B). In general, the interaction of transcritical and saddle-node bifurcations is also studied in other ecological systems, such as in Kooi et al. [116], Van Voorn and Kooi [189] and Saputra et al. [166].

Overall, we find that bistable region (grey colour) is larger in the IDE as compared to PDE models, which leads to more occurrences of priority effects under rapid dispersal levels. The three-species coexistence region (cyan colour) is also larger in IDE, where for different parameter values investigated, we observe stable coexistence of focal species (e.g. species 3) with its neighbouring competitors (e.g. species 1 and 2). We also notice that the width of the (yellow colour) region supporting two-species coexistence (e.g. with species 3 absence) outcome is wider in the PDE than IDE models. Ecologically, localised dispersal can cause a clumped spatial distribution (e.g. plants growing closely together) and a lower population density for focal species due to competition; consequently, this situation can in turn benefit the neighbouring competitors [92].

6.3.3 Contrasting Observations of Non-Local Dispersal on Species Presence-Absence in the Cases of Intermediate-Range and Long-Range Dispersal

In the previous section, we observe that the diversity of species is enhanced when dispersal occurs over non-adjacent spatial locations, whereas exclusion of some species occurs when dispersal is localised. This finding is illustrative, but it may not be general. The opposite observation is also possible: it has been observed in experimental studies [18] that species diversity is rapidly lost when dispersal occurs over larger scales, whereas species coexistence is possible when dispersal occurs over intermediate

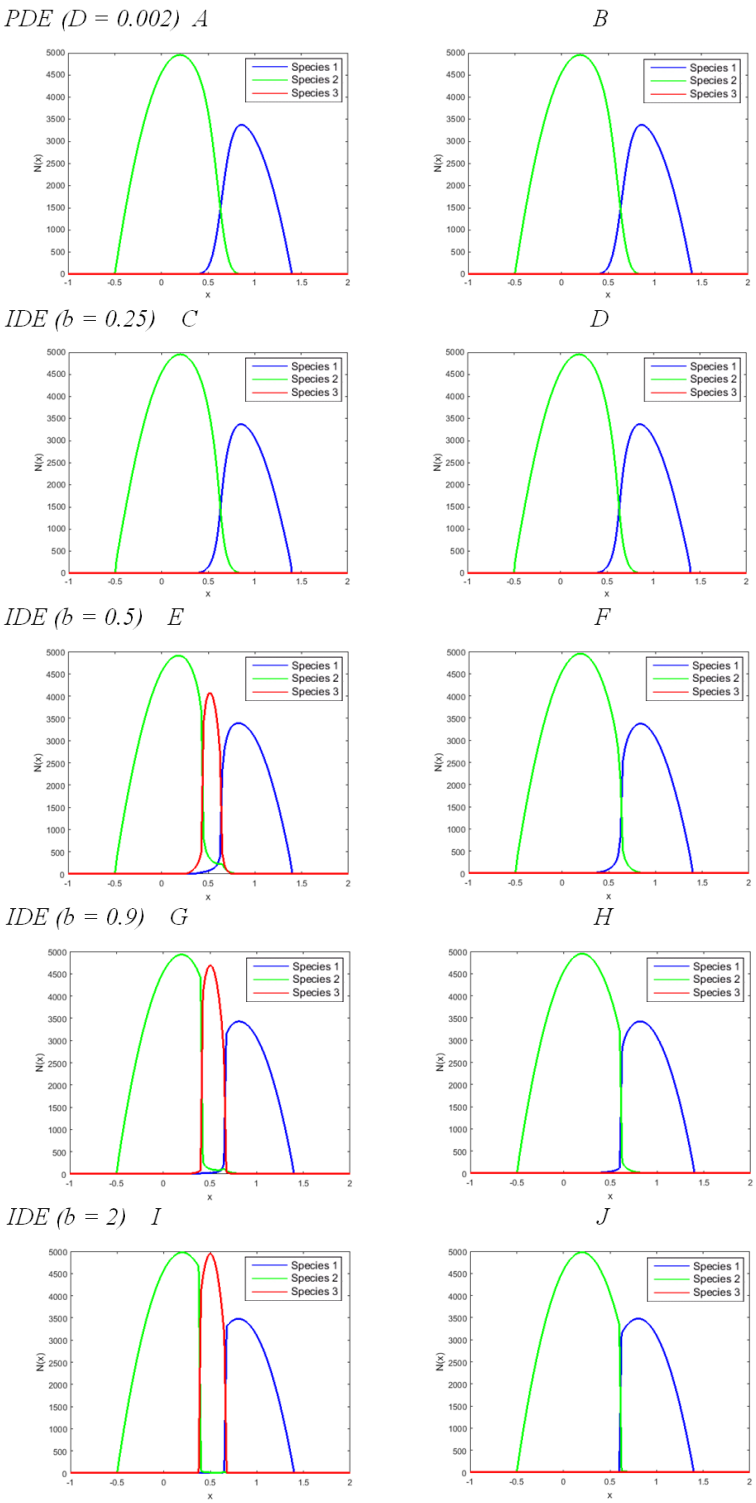


FIGURE 6.7: Results for stronger dispersal levels ($D = 0.002$) predicted by the PDE models (A,B); and the IDE models with $b = 0.25$ (C,D); $b = 0.5$ (E,F); $b = 0.9$ (G,H); $b = 2$ (I,J). *Left column*, species densities at $\alpha = 1.28$ when initial abundances favour species 3: $N_1(x) = 0.1K_1(x), N_2(x) = 0.1K_2(x), N_3(x) = 0.9K_3(x)$. *Right column*, species densities at $\alpha = 1.28$ when initial abundances favour species 1 and 2: $N_1(x) = 0.9K_1(x), N_2(x) = 0.9K_2(x), N_3(x) = 0.1K_3(x)$. Carrying capacities are as in Figure 6.1. These plots are computed by numerical simulation with MATLAB `ode15s` solver.

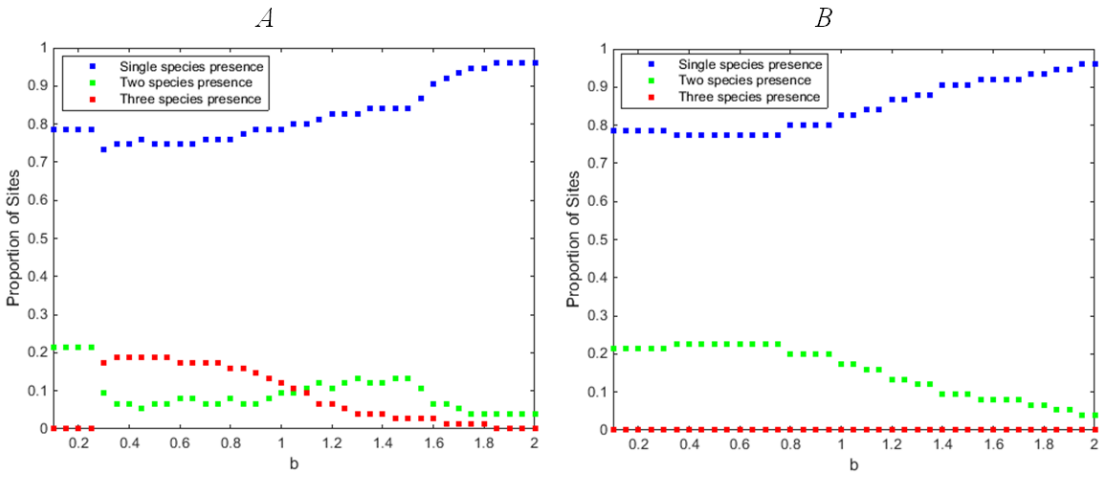


FIGURE 6.8: Proportion of different species present across sites x for different values of b: single-species present (blue squares); two-species present (green squares); three-species present (red squares). Stack graphs for the IDE models with stronger dispersal levels ($D = 0.002$) at $\alpha = 1.28$ as dispersal distance b changes. *Left*, IDE results when initial abundances favour species 3: $N_1(x) = 0.1K_1(x), N_2(x) = 0.1K_2(x), N_3(x) = 0.9K_3(x)$. *Right*, IDE results when initial abundances favour species 1 and 2: $N_1(x) = 0.9K_1(x), N_2(x) = 0.9K_2(x), N_3(x) = 0.1K_3(x)$. Carrying capacities are as in Figure 6.1. These plots are computed by numerical simulation with MATLAB `ode15s` solver.

or short distances; in the latter case, species diversity peaks at intermediate-range dispersal. Motivated by this experimental observation, we investigate the consequences of intermediate-range and long-range dispersal on species coexistence using our non-local dispersal model (6.1). To do this, we conducted numerical experiments by considering various dispersal distance b and also different initial species abundances. For example, Figure 6.7 shows the presence-absence of species at $\alpha = 1.28$ for stronger dispersal levels ($D = 0.002$) predicted by the PDE (first row), and the IDE models with $b = 0.25$ (second row), $b = 0.5$ (third row), $b = 0.9$ (fourth row) and $b = 2$ (fifth row). These plots are generated using two different initial conditions: initial abundances favour species 3 (left column); and initial abundances favour species 1 and 2 (right column). We also constructed stack graphs for the IDE models, which are shown in Figure 6.8, for a range of values of dispersal distance b. These plots summarise the proportion of different species present across sites x (e.g. single-species present (blue squares), two-species present (green squares) and three-species present (red squares)) as dispersal distance b changes. To generate these stack graphs, we used two different initial conditions: initial abundances favour species 3 (left column); and initial abundances favour species 1 and 2 (right column). As with the summary plots, we define a

species to be present if its density is greater than 0.5% of the maximum density of that species.

When b is relatively small, the predictions of the IDE (Figure 6.7C, D) are in agreement with those of the PDE (Figure 6.7A, B); in the case of stronger dispersal, priority effects disappear and coexistence of two-species are possible near the central region. When b increases to intermediate levels, we find that priority effects emerge with coexistence of three (Figure 6.7E, G) or two species (Figure 6.7F, H) occurs near the centre of the region depending on initial abundances. The occurrence of priority effects is still evident when b is relatively large (Figure 6.7I, J), but we observe more outcomes where species exclusions are possible; in this situation, mostly one species dominating at any given location x, depending on initial abundances. This observation can clearly be seen from our stack graphs (Figure 6.8A): when non-local dispersal process occurs over very large spatial scales (e.g. $b = 2$), multi-species coexistence is impossible. In this situation, the proportion of sites with only one-species (blue squares) present increases rapidly, while the sites with two-species (green squares) and three-species (red squares) present reduce to low proportions. We also observe that non-local dispersal that occurs over intermediate distances (e.g. $b = 0.5$) can promote multi-species coexistence in comparison to non-local dispersal over short distances (e.g. $b = 0.25$) or purely local dispersal. For short-range dispersal, priority effects vanish in our stack graphs, and only two-species coexistence is possible for different initial abundances (Figure 6.8A, B).

To investigate the disappearance of priority effects as the values of b change, we performed numerical continuation to track the steady states of the IDE models. Figure 6.9 depicts the steady-state density of species 3 at $x = 0.5$ for stronger dispersal levels ($D = 0.002$) when $\alpha = 1.28$ as parameter b in the IDE is varied. There are three branches of steady states: the upper (species 3 present) and lower branches (species 3 absent) of steady states are stable (blue curves); these are separated by an unstable steady state (red curve). There is a threshold dispersal distance b_T, corresponding to a saddle-node bifurcation, below which the upper branch of steady states vanishes and priority effects vanish. For values of dispersal distance $b < b_T$, the priority effects disappear and there is only one stable steady state, in which species 3 is absent. For values

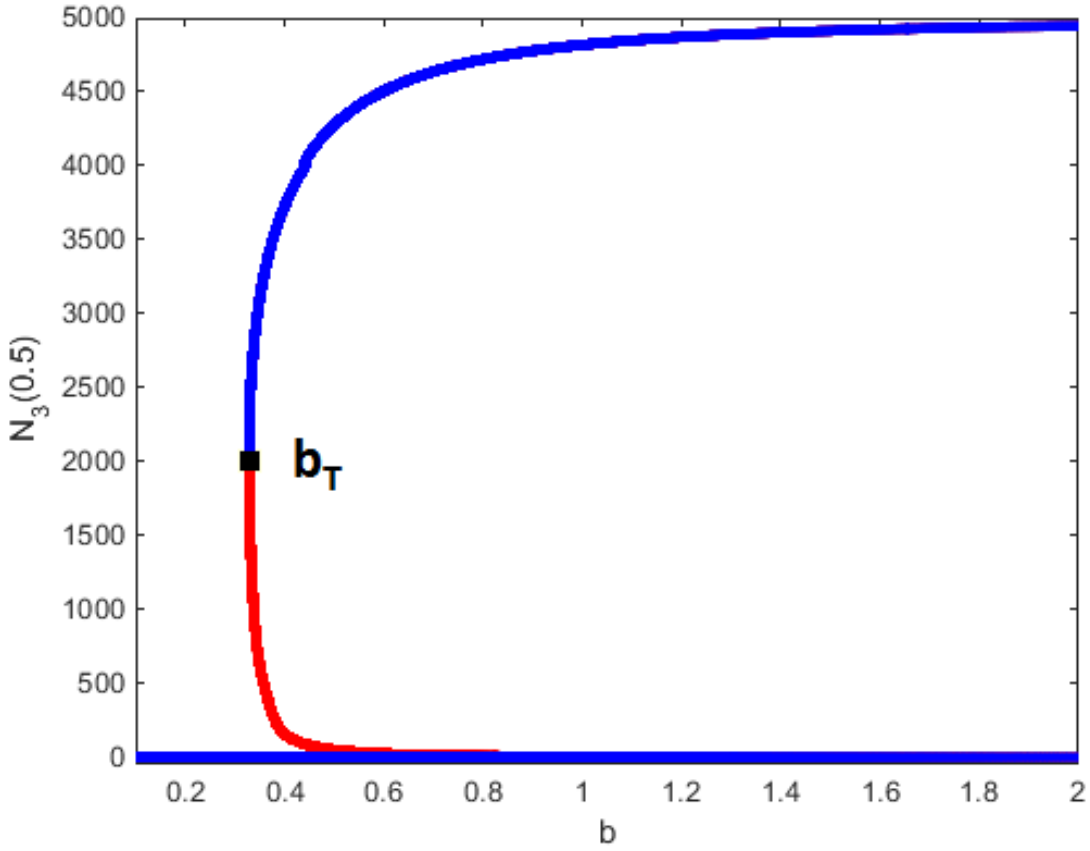


FIGURE 6.9: The density of a focal species (species 3) at $x = 0.5$ and $\alpha = 1.28$ for IDE models with stronger dispersal levels ($D = 0.002$) as the dispersal distance b changes. The threshold value b_T (black square) corresponds to saddle-node bifurcation point. There are three branches of N_3: (i) unstable steady-states (red curves); (ii) stable steady-state, with species 3 presence (upper blue curves); (iii) stable steady-state, with species 3 absence (lower blue curves). Other parameter values as in Table (6.1). These plots are computed by numerical continuation using XPPAUT.

of dispersal distance $b > b_T$, priority effects occur and the density N_3 tends toward upper or lower steady-state, depending on initial species abundances.

6.4 Discussion and Ecological Implications

In this chapter, we have used PDE and IDE models to study the influences of different dispersal mechanisms on the occurrence of priority effects, which are mediated by intense biotic interactions across heterogeneous environments. We discover that the occurrence of priority effects vary with dispersal strength and they are eliminated at stronger values of dispersal in the IDE than in the PDE models. Our summary plots show that the regions supporting dispersal-mediated coexistence and/or priority effects are wider in the IDE models under rapid dispersal scenario. These findings demonstrate that priority effects, which can mediate multi-species coexistence, are more pronounced in the non-local dispersal models. It has been shown that non-local dispersal process can enhance the chance of species survival across heterogeneous environments [49]. Biologically, non-local dispersal increases the possibility of migrating species to escape the effects of intense biotic interactions from other species by dispersing further away; this situation enhances the establishment and persistence of species [48], [49]. We also notice that dispersal-induced extinction phenomenon is more evident in the PDE models, which leads to extinction of some species near the centre at more values of D. Local dispersal generates a clumped spatial distribution, which increases the effects of competition among species and enhances the possibility of species extinction [48].

We also demonstrate the important roles of the spatial scale of ecological processes in maintaining species diversity (Figure 6.7, Figure 6.8 and Figure 6.9). As discussed in Section 1.1, experimental studies [114], [160] illustrate that allowing ecological processes such as dispersal to occur locally can promote diversity in a community assembly [160]; however, when ecological processes occur over very large spatial scale, species diversity is rapidly lost and extinction is possible [114]. Our findings are in line

with the aforementioned observations: we observe that while very long-range dispersal can lead to an exclusion effect (of all but one species), short-range and intermediate-range dispersal can promote coexistence of two and three species, respectively. Ecologically, long-distance dispersal increases the risk of landing in unsuitable habitats outside species fundamental niches [87], [201]. In our models, this effect can be seen in the case of neighbouring competitors (e.g. species 1 and 2); consequently, this situation reduces the possibility of multiple species to coexist, and in turn benefit focal species (e.g. species 3), in which they can exclude other competitors near the central region. In general, these findings have qualitative implications in the maintenance of species diversity: if our community models are representative of those in natural communities, then we might expect the scale in which dispersal occurs matter in determining the presence-absence of species. Therefore, we suggest that understanding the diversity of species requires explicit consideration of dispersal process occurring at different scales rather than at a local scale only.

Our continuation results further reveal the bifurcation structure of the PDE and IDE models and they are consistent with simulation results. We find that (Figure 6.4) there ia a threshold dispersal strength D: this threshold value depends on the modes of dispersal and we show that this value is higher in the IDE model than in the PDE model by considering the dynamics near the central region. Consequently, priority effects persist for stronger dispersal in IDE model, as opposed to PDE model. These findings also demonstrate the possibility of dramatic changes on species presence-absence in response to small variations in the ecologically-relevant parameters, which can induce an uncertainty in the range-limit predictions. Therefore, to produce robust predictions about which species will be present (or absent) across a geographical region, this may require accurate knowledge of dispersal rates and biotic interactions, as well as information on dispersal modes of species.

Taken together, the presence-absence of species is shaped by numerous factors, including abiotic environmental conditions, biotic interactions and migration patterns. The occurrence of priority effects depends on the modes and magnitude of dispersal, and also strength of biotic interactions. For short-range dispersal patterns, the predictions of priority effects using local dispersal (PDE) models are in agreement with those

of non-local dispersal (IDE) models, particularly for moderate dispersal strength. Increasing dispersal strength leads to different predictions on the occurrence of priority effects in these two models. Both continuation and simulation results show that priority effects are more pronounced in the non-local dispersal models than in the local dispersal models. It has also been shown that non-local dispersal can have different effects on presence-absence of species: although very long-range dispersal can result in exclusion of species, intermediate-range dispersal can permit multi-species coexistence in comparison to short-range dispersal (or purely local dispersal).

In conclusion, this study serves as a first step in demonstrating how incorporation of different dispersal patterns can improve our predictions of priority effects that strongly determine the presence-absence of species. Knowledge of local and non-local dispersal mechanisms can be incorporated in developing robust predictive models for estimating potential presence-absence of species. We recommend the use of local dispersal (PDE) models to predict the combined effects of dispersal, environment and biotic interactions on range limits when species' dispersal ability are localised. However, we suggest that the range-limit predictions will be revealed better by non-local dispersal (IDE) models when considering certain target species that can disperse larger distances via non-local dispersal.

Chapter 7

Two-Dimensional Space Models

7.1 Introduction

In this chapter, we ask the following questions:

- Do our results on species presence-absence change when each species' abiotic requirements are described by more than one variable?
- If presence-absence depends on two variables, how do our predictions change if one of them is ignored?

To address these problems, we investigate multi-species community dynamics using two-dimensional (2-D) space. That is, environmental suitability for each species depends on two variables, rather than one. Our aim is to develop an understanding of when an ecological prediction is similar in the 1-D and the 2-D space models, with respect to the occurrence of priority effects and species coexistence. We will use the term "dimensionality of space" to represent the spatial dimension of an ecological system (i.e. community dynamics in one-dimensional (1-D) or two-dimensional (2-D) space). This exploration is inspired by different studies, which show that 1-D and 2-D space models can exhibit qualitatively different predictions about species persistence [135], [144], [197]. It has been demonstrated that species extinction is more likely in the 1-D model, compared to the 2-D space model [144]. Comparative studies between the 1-D and 2-D space models discussed in Chapter 2 show that addition of a second space dimension can influence species persistence and coexistence [135], [197]. Motivated by these observations, we extend studies consisting of biotic interactions and environmental gradients [133], [164] to incorporate a local dispersal through the 2-D diffusion process [23], [69], [70]. This inclusion leads to a system of partial-differential equations

(PDE) in the 2-D space. We examine the consequences of different dimensionality of space on the occurrence of priority effects by comparing simulation results of 1-D with 2-D models under varying dispersal strength. We discover that as well as a pronounced increase in system complexity, adding a second space dimension modifies the strength of priority effect. The observations of priority effects are either qualitatively similar in both models, or they are strengthened or weakened, depending on the differences in species environmental suitability and magnitude of dispersal. We also observe more outcomes where multiple species coexistence is possible as dimensionality of space is increased.

7.2 The 1-D and 2-D Space Deterministic Models with Local Dispersal

We consider partial differential equations (PDE) models for the densities N_i of m species in 1-D ($0 \leq x \leq 1$) and 2-D ($0 \leq x, y \leq 1$) domains:

$$\frac{\partial N_i}{\partial t} = \frac{r_i N_i}{K_i(x,y)} \left(K_i(x,y) - \sum_{j=1}^{m} \alpha_{ij} N_j \right) + D_i \nabla^2 N_i \qquad (i = 1, 2, ..., m) \tag{7.1}$$

The suitability of environments or locations is modelled by allowing each species' carrying capacity $K_i(x, y)$ to vary with spatial locations x and y. The variables x and y could be locations within a geographical region, or used as a proxy for abiotic environmental factors that affect the presence-absence of species such as temperature, moisture or elevation. The effects of biotic interactions on range limits depend on how each species responds to the environmental gradients. We use nonlinear environmental gradients in a three-species model ($m = 3$) of a multi-species community. We let the carrying capacities of species 1 and 2 vary with x, while the carrying capacity of species 3 varies with y, as described by the following equations:

$$K_1(x,y) = \max \left\{ K_{1,max} \left(1 - \frac{(x - x_1)^2}{w_1^2} \right), 0.001 \right\} \tag{7.2}$$

$$K_2(x,y) = \max\left\{K_{2,max}\left(1 - \frac{(x-x_2)^2}{w_2^2}\right), 0.001\right\} \tag{7.3}$$

$$K_3(x,y) = \max\left\{K_{3,max}\left(1 - \frac{(y-y_3)^2}{w_3^2}\right), 0.001\right\} \tag{7.4}$$

where x_i and y_i are the locations at which the carrying capacity for species i is at its maximum $K_{i,max}$ and w_i is the width of the fundamental niche. To ensure equations (7.2,7.3,7.4) are well defined, we have set K_i to a small but non-zero value (0.001) outside the fundamental niche. For visualisation of carrying capacities of species 1, 2 and 3 in the 2-D model described by equations (7.2,7.3,7.4), refer to Figure 7.1A, C and E, respectively.

The diffusion term models dispersal among locations, with the parameter D_i representing the strength of dispersal for species i. We assume that interacting species have the same dispersal rate ($D_i = D$) and no migration occurs across boundaries (by imposing zero-flux boundary conditions for each species):

$$\left.\frac{\partial N_i}{\partial x}\right|_{x=0,1} = \left.\frac{\partial N_i}{\partial y}\right|_{y=0,1} = 0. \tag{7.5}$$

We performed numerical simulations for the 1-D and 2-D space models and the results of the two models are compared in the next sections. In particular, we sampled our 2-D results by taking a series of slices at fixed values of x and y, and compared with the results from a 1-D model with identical carrying capacity. To illustrate our observations, we presented the results for three different slices as an example; these slices are shown using black lines in the 2-D plots of species' carrying capacities (Figure 7.1A,C,E), and the corresponding 1-D plots of carrying capacities are as follows:

(i) **Slice 1 - horizontal slice at** $y = 0.5$ (Figure 7.1B)

Competitive environments between a generalist species (e.g. species 3) with very high carrying capacity and wide environmental tolerance and two specialist species (e.g. species 1 and species 2) where their carrying capacities vary across locations x.

(ii) **Slice 2 - vertical slice at** $x = 0.6$ (Figure 7.1D)

Competitive environments between a specialist species (e.g. species 3) with K_i *varies with*

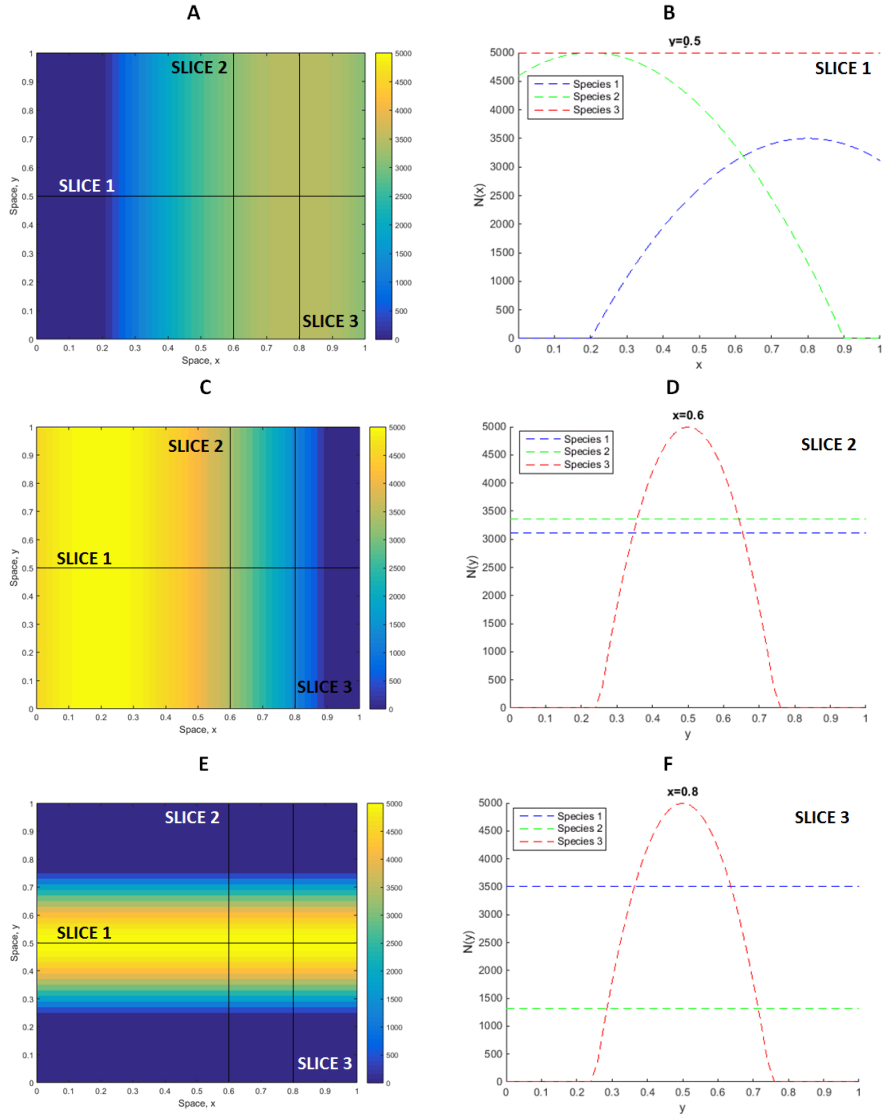


FIGURE 7.1: Carrying capacities in the 2-D and 1-D models: species 1 (A), species 2 (C) and species 3 (E). Black lines in (A,C,E) correspond to different slicing at fixed values of x or y performed on species' carrying capacities in the 2-D models: (i) slice 1 (horizontal slice at $y = 0.5$); (ii) slice 2 (vertical slice at $x = 0.6$); and (iii) slice 3 (vertical slice at $x = 0.8$). The corresponding 1-D plots of carrying capacities are illustrated in B, D and F.

*y and two generalist species (e.g. species 1 and 2) with K_i constant across y. In this case, there are **small differences between environmental suitability** of generalist species.*

(iii) **Slice 3 - vertical slice at** $x = 0.8$ (Figure 7.1F)

*Competitive environments between a specialist species (e.g. species 3) with K_i varies with y and two generalist species (e.g. species 1 and 2) with K_i constant across y.In this case, there are **large differences between environmental suitability** of generalist species.*

7.2.1 Numerical Methods

Equation (7.1) is solved numerically over the domain $0 \leq x, y \leq 1$ using the method of lines. The method of lines involved a discretisation of spatial variables x and y into a uniform grid in both dimensions with mesh size h. This leads to a mesh with $A_x + 1$ nodes along the x direction and A_y+1 nodes along the y direction. Let us denote $N_{j,k}$ as the approximation of solution at the node (x_j, y_k) of the spatial grid with $j = 0, 1, ..., A_x$ and $k = 0, 1, ..., A_y$. The spatial derivatives in equation (7.1) are replaced by second central difference approximations:

$$\nabla^2 N_{j,k} = \frac{N_{j+1,k} + N_{j-1,k} + N_{j,k+1} + N_{j,k-1} - 4N_{j,k}}{h^2} \tag{7.6}$$

The zero-flux boundary conditions (7.5) are coded in the equations for the end points using a central difference approximation. This results in a system of ODE, which is solved for steady state by a standard ODE solver, `ode15s` for $t = 1000$. We used $h = 2 \times 10^{-2}$ and initial conditions as indicated in each figure section. The results are insensitive to a reduction in grid spacing h. Unless otherwise stated, parameter values used in the simulation are given in Table (7.1).

7.3 Results

In general, the occurrence of priority effects depends on the intensity of biotic interactions (α). When $\alpha < 1$ (i.e. interspecific competition is weaker than intraspecific), this situation leads to coexistence of species in both models. For instance, the first three rows of Figure 7.2 show the 2-D PDE results at $\alpha = 0.8$ for $D = 0.0015$ (first column) and $D = 0.004$ (second column). We observe that species coexistence is possible

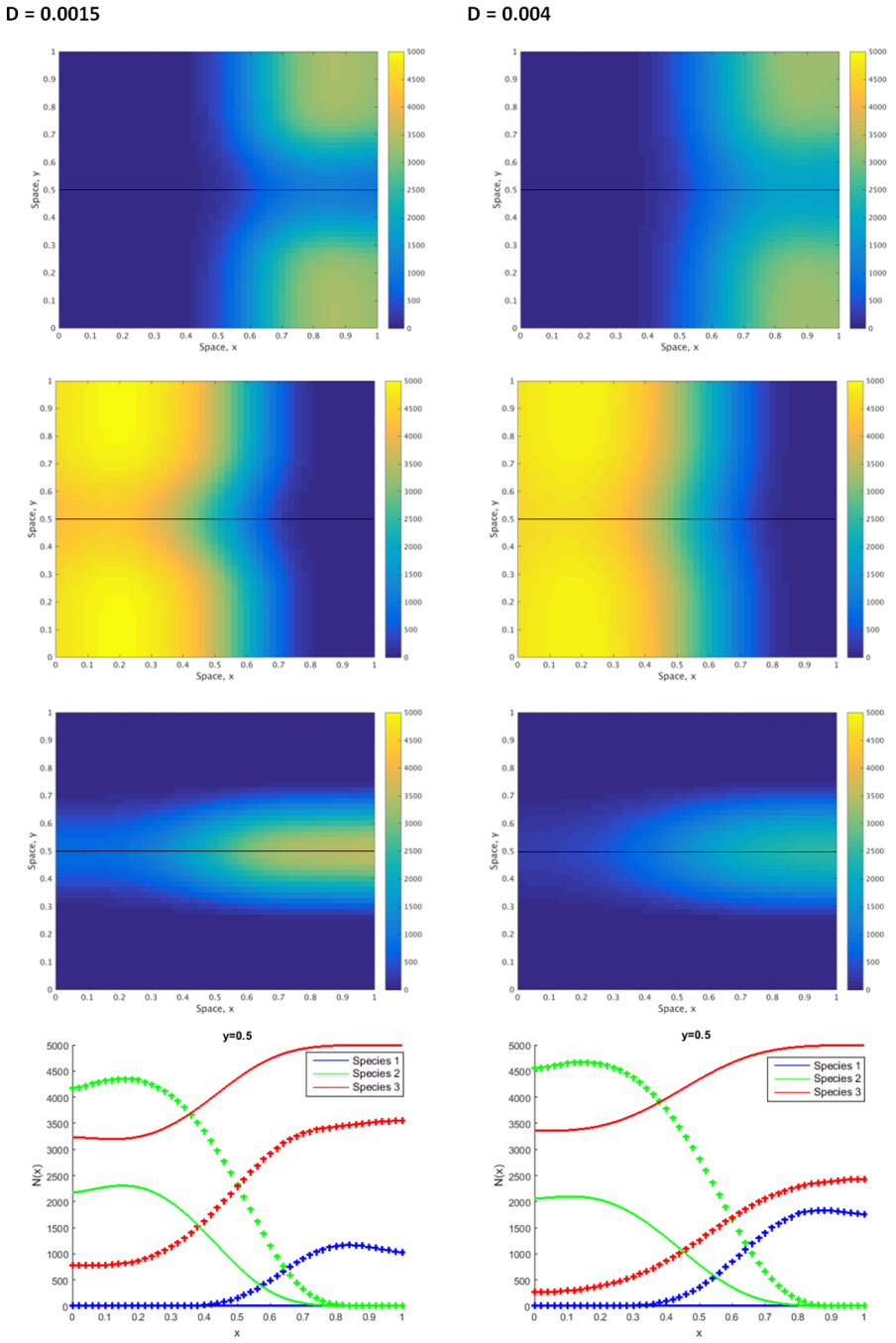


FIGURE 7.2: Results of the models in 1-D and 2-D space when $\alpha = 0.8$ under under different dispersal scenarios: $D = 0.0015$ (first column); $D = 0.004$ (second column). First three rows represent the densities of different species: species 1 (first row); species 2 (second row); species 3 (third row). Blue, green and yellow colours correspond to very low, moderate and high species densities, respectively. To compare the dynamics between the two models, horizontal slicing at $y = 0.5$ (slice 1) are performed to the 2-D predictions; these results from slice 1 (plus signs) and the corresponding results from 1-D model (solid lines) are plotted together in the last row. Carrying capacities are as in Figure 7.1. These plots are computed by numerical simulation with MATLAB `ode15s` solver.

TABLE 7.1: Parameter values.

Symbol	Description	Parameter Values
r_i	The intrinsic growth rate of species i	1
$K_{1,max}$	As indicated in equation (7.2)	3500
$K_{2,max}$	As indicated in equation (7.3)	5000
$K_{3,max}$	As indicated in equation (7.4)	5000
x_1	As indicated in equation (7.2)	0.8
x_2	As indicated in equation (7.3)	0.2
x_3	As indicated in equation (7.4)	0.5
w_1	As indicated in equation (7.2)	0.6
w_2	As indicated in equation (7.3)	0.7
w_3	As indicated in equation (7.4)	0.25
D_i	Diffusion coefficient	0.0015-0.004
α_{ij}	Competition coefficient (values given in figure captions)	

near the central region in the 2-D models. In the last row of Figure 7.2, we show the predictions of the 2-D models (plus signs) at slice 1 (black lines); for comparison, the corresponding predictions of the 1-D models are also shown using solid lines. Overall, we find that the 2-D model demonstrates three-species coexistence outcomes, whereas the corresponding 1-D model exhibits two-species coexistence for different dispersal strength.

When $\alpha > 1$ (i.e. interspecific competition is stronger than intraspecific), priority effects can occur with the range limits of species depend on initial abundances in both models. In the absence of dispersal, competitive exclusion of all but one species occurs; inclusion of dispersal into the models reduces competitive exclusion effect that occurs in no-dispersal case and promotes coexistence of species. In the following sections, we compare the results of the two models and investigate whether the 1-D and the 2-D space models yield qualitatively similar predictions of priority effects under relatively moderate ($D = 0.0015$) and rapid ($D = 0.004$) dispersal levels. We highlight the similarities and differences between the predictions from the 1-D and 2-D models, with respect to the occurrence of priority effects and species coexistence. In particular, we illustrate how the predictions of priority effects can vary in these two models depending on species environmental suitability and dispersal intensity.

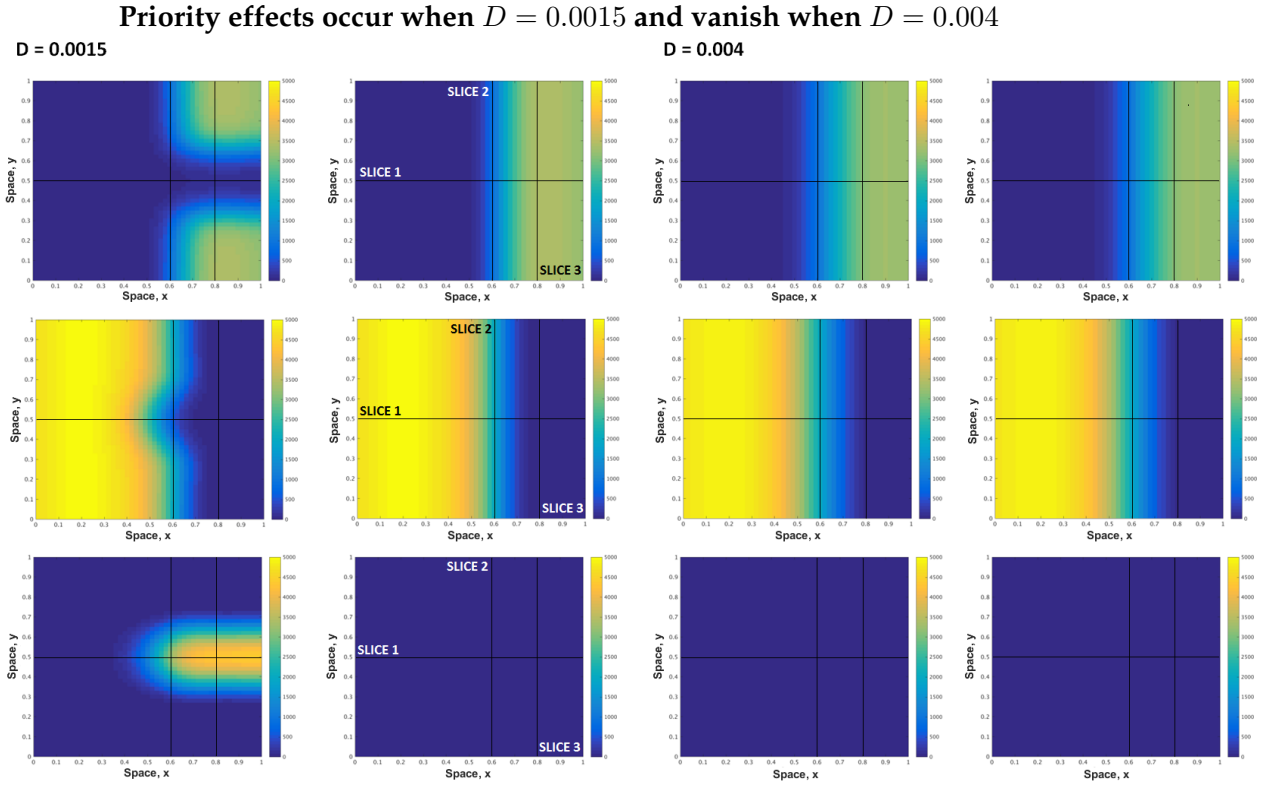


FIGURE 7.3: Results of the models in two-dimensional space when $\alpha = 1.5$ under different dispersal strength: $D = 0.0015$ (first and second columns); $D = 0.004$ (third and fourth columns). Each row represents the densities of different species: species 1 (first row); species 2 (second row); species 3 (third row). Blue, green and yellow colours correspond to very low, moderate and high species densities, respectively. *First and third columns*, snapshots of the 2-D model when initial abundances favour species 3: $N_1(x,y) = 0.1K_1(x,y), N_2(x,y) = 0.1K_2(x,y), N_3(x,y) = 0.9K_3(x,y)$. *Second and fourth columns*, snapshots of the 2-D model when initial abundances favour species 1 and 2: $N_1(x,y) = 0.9K_1(x,y), N_2(x,y) = 0.9K_2(x,y), N_3(x,y) = 0.1K_3(x,y)$. Black lines correspond to different slicing performed on the 2-D results: (i) slice 1 (horizontal slice at $y = 0.5$); (ii) slice 2 (vertical slice at $x = 0.6$); and (iii) slice 3 (vertical slice at $x = 0.8$). Carrying capacities are as in Figure 7.1. These plots are computed by numerical simulation with MATLAB `ode15s` solver.

7.3.1 When the predictions of priority effects are more pronounced in the 2-D models than in the 1-D models

Figure 7.3 shows the 2-D PDE results at $\alpha = 1.5$ in which each row represents the density of different species (first to third row: species 1, 2 and 3, respectively). The first (respectively, last) two columns show the 2-D results when $D = 0.0015$ (respectively, $D = 0.004$). These plots are generated using two different initial abundances: initial abundances favour species 3 (first and third columns); and initial abundances favour species 1 and 2 (second and fourth columns). We have also investigated the outcomes of the 2-D model using different initial abundances (e.g. initial abundances

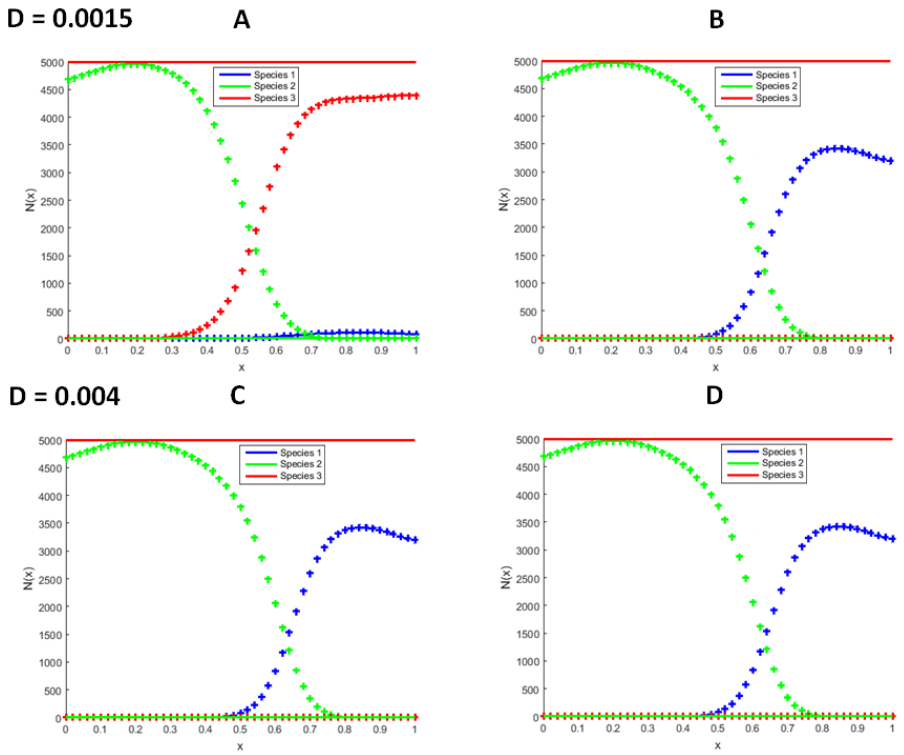


FIGURE 7.4: Results of the models in 1-D (solid lines) and 2-D (plus signs) space when $\alpha = 1.5$ under different dispersal strength: $D = 0.0015$ (A,B); $D = 0.004$ (C,D). The 2-D results correspond to slice 1 (horizontal slicing at $y = 0.5$) of Figure 7.3. These plots are generated using different initial abundances: initial abundances favour species 3, $N_1(x,y) = 0.1K_1(x,y), N_2(x,y) = 0.1K_2(x,y), N_3(x,y) = 0.9K_3(x,y)$ (left column); and initial abundances favour species 1 and 2, $N_1(x,y) = 0.9K_1(x,y), N_2(x,y) = 0.9K_2(x,y), N_3(x,y) = 0.1K_3(x,y)$ (right column). Carrying capacities are as in Figure 7.1B. These plots are computed by numerical simulation with MATLAB `ode15s` solver.

favour species 1 and 3; initial abundances favour species 2 and 3; initial abundances favour species 1; and initial abundances favour species 2); the outcomes are similar to the results shown in Figure 7.3. For relatively moderate dispersal levels (e.g. $D = 0.0015$), this situation leads to the occurrence of priority effects and promotes multiple species coexistence (compare the first two columns of Figure 7.3). Increasing dispersal strength (e.g. $D = 0.004$) leads to the disappearance of priority effects (compare last two columns of Figure 7.3); consequently, rapid dispersal causes extinction of some species (e.g. species 3).

Closer comparison of the 2-D results at slice 1 with the corresponding results from the 1-D models with identical carrying capacity in Figure 7.4 reveals some interesting observations. For different initial abundances, we observe no priority effects in the 1-D model (solid lines); in this situation, competitive exclusion occurs with the generalist

dominating across the whole locations (compare solid lines in Figure 7.4). However, in the 2-D model, we observe qualitatively different dynamics (compare plus signs in Figure 7.4). In particular, the 2-D model predicts priority effects when $D = 0.0015$ (Figure 7.4A,B) with two possible outcomes:

(i) coexistence of specialists-generalist e.g. species 2 and 3 (Figure 7.4A);

(ii) coexistence of both specialists e.g. species 1 and 2 (Figure 7.4B).

Overall, these observations demonstrate that priority effects are more pronounced in the 2-D model than in the 1-D model. Increasing dispersal intensity ($D = 0.004$) leads to further disagreement between the two models (Figure 7.4C, D). While the 1-D model (solid lines) predicts that generalist survives throughout the whole locations, rapid dispersal causes priority effects to vanish in the 2-D model (plus sign) and leads to exclusion of generalist species. Consequently, only coexistence of both specialists is possible in the 2-D model at higher dispersal levels.

7.3.2 When the predictions of priority effects are less pronounced in the 2-D models than in the 1-D models

The above analysis illustrates conditions under which the observations of priority effects are strengthened in the 2-D model than in the 1-D model. The opposite observation is also possible, and this result is discussed using slice 2 (Figure 7.1D) as an example. We find that priority effects are more prevalent in the 1-D models compared to the 2-D models when there are small differences between species environmental suitability. To illustrate this observation, consider Figure 7.5, which shows the 1-D (solid lines) and 2-D results (plus signs) with each row representing a different strength of dispersal: $D = 0.0015$ (first row); and $D = 0.004$ (second row). These results are generated using three different initial species abundances: initial abundances favour species 1 and 3 (first column); initial abundances favour species 2 and 3 (second column); and initial abundances favour species 1 and 2 (third column). Environmental suitability of species for this scenario is shown in Figure 7.1D using slice 2. In general, this situation corresponds to competitive environments between two generalist species (e.g. species

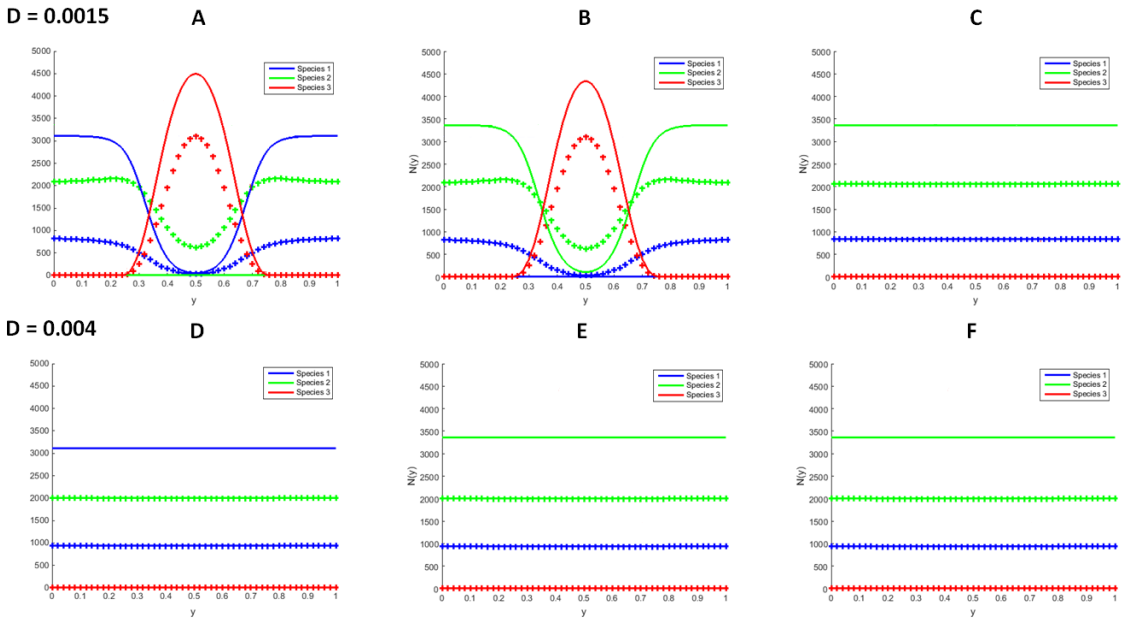


FIGURE 7.5: Results of the models in 1-D (solid lines) and 2-D (plus signs) space when $\alpha = 1.5$ under different dispersal strength: $D = 0.0015$ (A,B,C); $D = 0.004$ (D,E,F). The 2-D results correspond to slice 2 (vertical slicing at $x = 0.6$) of Figure 7.3. These plots are generated using different initial abundances: initial abundances favour species 1 and 3, $N_1(x,y) = 0.9K_1(x,y), N_2(x,y) = 0.1K_2(x,y), N_3(x,y) = 0.9K_3(x,y)$ (left column); initial abundances favour species 2 and 3, $N_1(x,y) = 0.1K_1(x,y), N_2(x,y) = 0.9K_2(x,y), N_3(x,y) = 0.9K_3(x,y)$ (centre column); and initial abundances favour species 1 and 2, $N_1(x,y) = 0.9K_1(x,y), N_2(x,y) = 0.9K_2(x,y), N_3(x,y) = 0.1K_3(x,y)$ (right column). Carrying capacities are as in Figure 7.1D. These plots are computed by numerical simulation with MATLAB `ode15s` solver.

1 and 2) with K_i constant across y and a specialist species (e.g. species 3) with K_i varies with y.

Here, small differences between environmental suitability of species (compare dotted lines of generalists in the presence of specialist in Figure 7.1D) lead to disagreement on the predictions of the two models, with priority effects more pronounced in the 1-D model (solid lines) than in the 2-D model (plus signs). For relatively moderate dispersal ($D = 0.0015$), the 1-D model (solid lines) shows priority effects with tri-stable behaviour near the central region:

(i) coexistence of generalist-specialist e.g. species 1 and 3 (Figure 7.5A);

(ii) coexistence of generalist-specialist e.g. species 2 and 3 (Figure 7.5B);

(iii) persistence of dominant generalist e.g. species 2 (Figure 7.5C).

This observation contrasts with the prediction of the 2-D model (plus signs); in this case, the 2-D model shows bi-stable behaviour near the centre:

(i) multi-species coexistence (Figure 7.5A, B);

(ii) coexistence of both generalists (Figure 7.5C).

We also find that coexistence of both generalists is the only possible outcome in the 2-D model (plus signs) when $D = 0.004$ for different initial abundances (Figure 7.5D, E, F). In this case, priority effects are weakened in the 2-D model as dispersal intensity increases. However, in the 1-D model (solid lines), priority effects persist in which competitive exclusion occurs with either one of the generalist species survives throughout the entire locations.

7.3.3 When the predictions of priority effects are similar in the 1-D and the 2-D models

In contrast to the previous observation, we also find that the predictions of priority effects are similar in these two models when there are large differences between species environmental suitability. To illustrate this observation, we use slice 3 (Figure 7.1F), and the results of the two models are shown in Figure 7.6 as an example. This figure depicts the 1-D (solid lines) and 2-D results (plus signs) with $D = 0.0015$ (first row) and $D = 0.004$ (second row) using two initial abundances: initial abundances favour species 3 (first column); and initial abundances favour species 1 and 2 (second column). Environmental suitability of species for this case is shown in Figure 7.1F. When differences in species environmental suitability are relatively large (compare dotted lines of generalists (e.g. species 1 and 2) in the presence of specialist (e.g. species 3) in Figure 7.1F), the predictions of priority effects from the 2-D model (plus signs) agree with those of the 1-D model (solid lines). For instance, priority effects occur when $D = 0.0015$ (Figure 7.6A, B) and lead to two different outcomes:

(i) coexistence of generalist-specialist e.g. species 1 and 3 (Figure 7.6 A)

(ii) persistence of dominant generalist e.g. species 1 (Figure 7.6 B).

When dispersal intensity increases (Figure 7.6C, D), we observe that priority effects disappear in both models. While it is observed that only dominant generalist survives

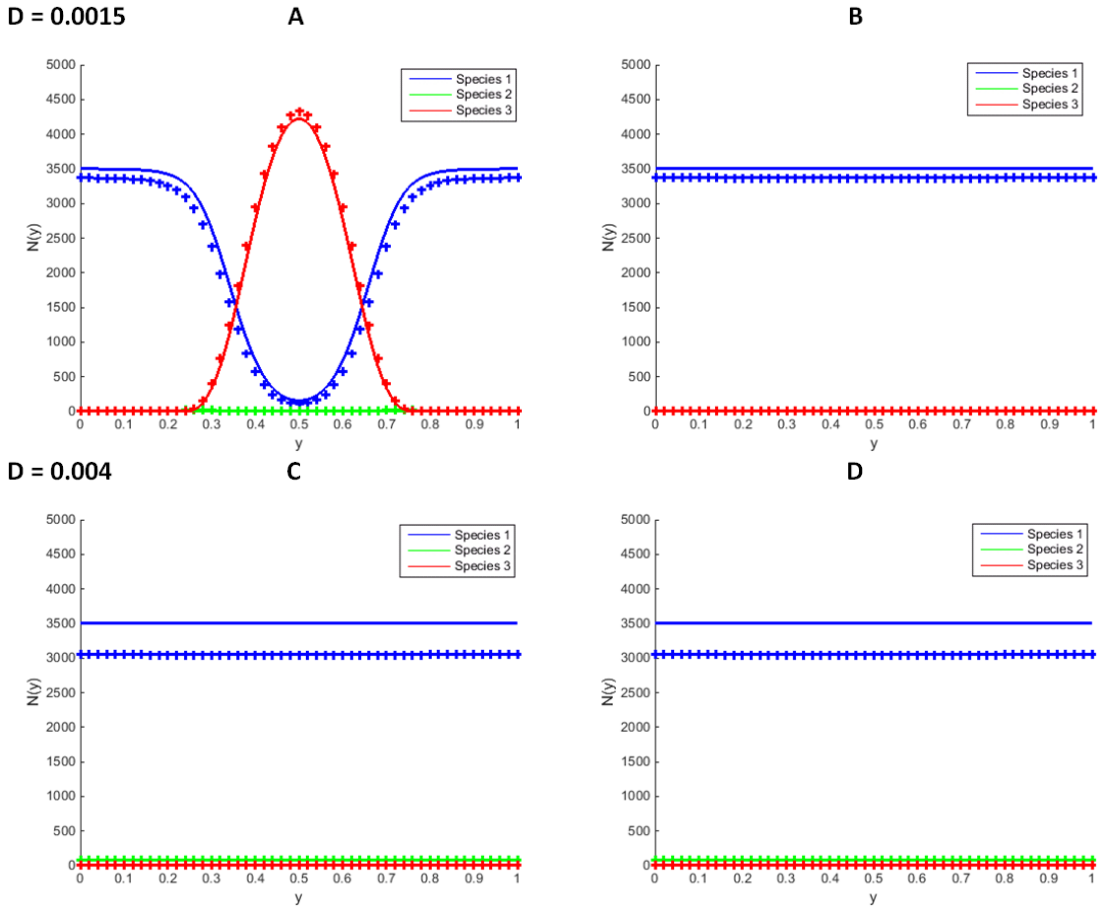


FIGURE 7.6: Results of the models in 1-D (solid lines) and 2-D (plus signs) space when $\alpha = 1.5$ under different dispersal strength: $D = 0.0015$ (A,B); $D = 0.004$ (C,D). The 2-D results correspond to slice 3 (vertical slicing at $x = 0.8$) of Figure 7.3. These plots are generated using different initial abundances: initial abundances favour species 3, $N_1(x,y) = 0.1K_1(x,y), N_2(x,y) = 0.1K_2(x,y), N_3(x,y) = 0.9K_3(x,y)$ (left column); and initial abundances favour species 1 and 2, $N_1(x,y) = 0.9K_1(x,y), N_2(x,y) = 0.9K_2(x,y), N_3(x,y) = 0.1K_3(x,y)$ (right column). Carrying capacities are as in Figure 7.1F. These plots are computed by numerical simulation with MATLAB `ode15s` solver.

in the 1-D model for different initial abundances, we find that coexistence of both generalists are possible in the 2-D model. This finding also supports our earlier observation (Figure 7.2) that the 2-D model permits more outcomes where species coexistence is possible, compared to the 1-D model.

7.4 Discussion and Ecological Implications

In this chapter, we demonstrate significant influences of species environmental suitability in a multi-species ecosystem consisting of biotic interactions and local dispersal. In particular, we investigate multi-species community dynamics in the presence of priority effects, and consider how this phenomenon and other ecological forces can jointly shape species presence-absence in the 1-D and 2-D space systems. Overall, we observe that the predictions of priority effects in these two models are either qualitatively similar, or they are weakened or strengthened, depending on how different species respond to environmental conditions and their dispersal intensity.

When biotic interactions are relatively weak ($\alpha < 1$), we observe more outcomes where multi-species coexistence is possible in the 2-D models compared to the 1-D models. In this case, while the 1-D models predict only two-species coexistence is possible, the 2-D predictions demonstrate the influential roles of dispersal of species from other locations to their neighbouring sites, which can promote multi-species coexistence. Based on these results, the use of 1-D models should be employed with caution when considering the influences of different abiotic environments and dispersal process on the presence-absence of species. This is because some target species may respond differently to a distinct set of environmental variables, and considering the influence of only one environmental component and ignoring the other abiotic variables could sometimes mislead us in predicting the potential presence-absence of dispersing species.

We also demonstrate that the observations of priority effects are similar in these two models when the differences in environmental suitability (i.e. K_i) of species are relatively large (Figure 7.6). In the system that we studied, this case corresponds to competition between two generalist species and a specialist species. We observe the

occurrence of priority effects in both models, with coexistence of generalist-specialist or persistence of dominant generalist are possible. We also find that small differences between environmental suitability of closely related species lead to different predictions between these two models (Figure 7.5): priority effects are more pronounced in the 1-D model than in the 2-D model. These observations on the influence of environmental suitability on the dynamics of ecological community are qualitatively similar to what previous studies have found using a lower-dimensional space model [69], [70]. As discussed in Chapter 3, Godsoe et al. [69] identify two biological mechanisms that can cause a significant change in the presence-absence of species: when there is a rapid (respectively, slow) change in competitive outcome between ecologically different (respectively, similar) species, small changes in the biology of species result in small (respectively, large) changes in the range limits of species.

When there is a small difference in environmental suitability of interacting species, this situation can induce an uncertainty in the predictions of species presence-absence. It has been observed that the 1-D system exhibits a high degree of sensitivity in the range-limit predictions (Figure 7.5); initial abundances affect species presence-absence, and the exclusions of all but one species occur through priority effects in some (or all) portions of space. In this case, we may require accurate information on biotic interactions, dispersal and initial species abundances as the range limits of species are hard to predict in the 1-D model. This sensitivity is softened by the inclusion of a second spatial dimension. The dynamics tend to stabilise in the 2-D model: higher-dimensional system predicts greater chance of species coexistence due to dispersal of interacting species from neighbouring sites. In some ecological communities, coexistence between closely related species has been observed [40], [175], and our results may help to explain this observation; in the system that we studied, coexistence of closely related species are possible due to the joint influences of dispersal and dimensionality of space. In this situation, we suggest that the range of possible outcomes will be revealed better by the 2-D models, as compared to 1-D models.

Additionally, we also highlight another important scenario of when the occurrence of priority effects differs in the two models. In particular, we illustrate that the observations of priority effects are more prevalent in the 2-D models than in the 1-D models

using an example of competitive interactions between a generalist and two specialist species (Figure 7.4). This situation occurs when generalist species has very high carrying capacity and wide environmental tolerance compared to its competitors. The 1-D models predict that coexistence of species is impossible, with only generalist species survives across the whole sites for different initial abundances. However, in the 2-D models, different combinations of coexisting species are observed, depending on initial species abundances and dispersal intensity. Dispersal from neighbouring locations with more abundant populations can sustain impoverished populations and facilitates coexistence of species [146]. From an ecological viewpoint, this finding is in line with rescue effect phenomenon from metapopulation theory. In metapopulation models, interacting species are assumed to occupy habitat patches that are connected by dispersal [9], [82]. It has been observed that coexistence of interacting species can occur in the metapopulation models due to rescue effects; in particular, dispersal of individuals from other habitat patches rescues the inferior species from being excluded [9]. For instance, experimental evidence using moss banks [71] has confirmed that dispersal can maintain the abundance of species within patches, and thus prevent species exclusion through rescue effects.

Overall, our work should serve as a starting point for studying how the impacts of dimensionality of space and dispersal can combine to result in species coexistence and the occurrence of priority effects that can strongly shape the range limits of species. We conclude that space dimensionality is a critical factor driving multi-species community dynamics. A better understanding of the effects of dimensionality will lead to a better estimate of species presence-absence and will build greater confidence in the models' predictions.

Chapter 8

Concluding Remarks

8.1 Conclusions

In this thesis, we have investigated the combined influences of different ecological forces namely biotic interactions, environmental components, dispersal and stochasticity on the range limits of multiple species. To do this, we employed deterministic and stochastic models, including interspecific competition, abiotic environments and dispersal terms. Our models predict species coexistence and the occurrence of priority effects over a substantial range of parameter values, suggesting that these results are not very sensitive to the specific choice of parameters. We find that the interaction of several ecological forces can strongly determine the occurrence of priority effects and species coexistence in multi-species communities. Our findings are novel because they contribute to understanding how local dispersal and demographic stochasticity determine when the presence-absence of species is predictable, as opposed to when it depends on biotic interactions and species establishment order. Our results also provide guidance on when dispersal process occurring at different scales matter in influencing coexistence of multiple species. Below we summarize our work, highlight the findings of the thesis, and discuss several ecological implications of our results.

We began with Chapter 2, which gives a general overview of selected models of population dynamics and dispersal process. We first derived several deterministic single-species models using stochastic process and then we discussed a model of biotic interactions, namely competition model. We showed how mathematical methods such as stability analysis and phase portraits can be used to analyse the possible competitive outcomes between species. We also showed how random walk theory can be

employed to establish the relationship between random walks as a description of local dispersal at individual-level and the diffusion equation as a description of local dispersal at population-level. We also discussed the concept of non-local dispersal, which can be used to model dispersal process that occurs over larger distances. Previous works and developments of different modelling frameworks are also presented in this chapter.

In Chapter 3, by using an ordinary-differential equations model, we showed that both biotic interactions and abiotic environments determine the range limits of multiple species. We derived analytical expressions for the range limits of species and we showed that our numerical simulation results are in agreement with analytical results. We also identified biological mechanisms that can significantly shift the range limits in multi-species communities. In the presence of priority effects, competitive exclusion occurs with only one species surviving at any given location. In this case, species range limits depend on initial abundances and we proposed a bio-control strategy based on these findings.

Chapter 4 explored the effects of local dispersal on our community dynamics using a partial-differential equations model. We found that dispersal substantially expands species ranges when biotic and abiotic forces are present; consequently, coexistence of species are possible. We also demonstrated that dispersal reduces competitive exclusion effects that occur in no-dispersal case and promotes coexistence of multiple species. Our results also show that priority effects are still evident in multi-species communities when dispersal is incorporated into the models. This observation of dispersal on priority effects is illustrative, but it may not be general. Other observations are also possible: in Chapter 5, we showed the conditions under which dispersal first enhances priority effects (i.e. for moderate dispersal), and then leads to their disappearance (i.e. for strong dispersal) in a multi-species community.

Additionally, in Chapter 5, we investigated the effects of stochasticity on the occurrence of priority effects using stochastic IBM. We demonstrated contrasting observations of stochasticity on priority effects: while this phenomenon is more prevalent in the stochastic IBM than in the deterministic models for large populations, we observed fewer occurrences of priority effects in IBM for small populations; in particular, we

realised that priority effects are eliminated by weaker values of dispersal when population sizes are small than when they are large.

Chapter 6 concerned with the effects of different dispersal patterns, namely local and non-local dispersal, on the predictions of priority effects. We illustrated that priority effects are more prevalent in the non-local dispersal models (i.e. integro-differential equations) than in the local dispersal models (i.e. partial-differential equations). Furthermore, we also found that non-local dispersal can have different effects on the presence-absence of species: although very long-range dispersal can result in exclusion of species, intermediate-range dispersal can permit multi-species coexistence in comparison to short-range dispersal or purely local dispersal.

Chapter 7 discussed the interaction of priority effects with dimensionality of space and local dispersal in shaping the presence-absence of species. By comparing simulation results from the 2-D space model with the 1-D space model, our findings suggested that knowledge on species' environmental suitability is crucial in order to improve our ability to predict the occurrence of priority effects across environments. In terms of species coexistence, we observed more outcomes where multiple species coexistence is possible in the 2-D space model compared to the 1-D space model.

Taken together, our findings demonstrate how different ecological forces driving species coexistence and priority effects can strongly shape the presence-absence of multiple species. In the absence of biotic interactions, abiotic environments determine the fundamental niches of species. Biotic interactions such as competition eliminate interacting species from some locations and affect their range limits. Dispersal affects species ranges in the presence of biotic and abiotic components. We also observe that multi-species coexistence are possible near the central region, with species diversity peaks at this location. Ecologically, this observation illustrates an example of a mid-domain effect, meaning that more species ranges overlap near the centre of a geographical region [30], [31]. This pattern of species diversity has been observed empirically; for instance, different studies of small mammals along elevational gradients observe patterns of mid-domain effect in which species diversity peaks at an intermediate elevation [137], [138].

The theoretical studies presented here also illustrate that dispersal can exert different impacts on community dynamics. One of the main findings of this thesis is the contrasting effects of dispersal in multi-species communities: dispersal-mediated coexistence and dispersal-induced extinction. This finding is consistent with a number of different studies, which show that dispersal can promote or hinder coexistence of species [21], [23], [46], [48], [160]. From a modelling point of view, our simulation results on the effects of dispersal on presence-absence of species can be considered as plausible phenomena since these common predictions are given by different modelling frameworks e.g. short-distance dispersal (PDE) model, long-distance dispersal (IDE) model, stochastic (individual-based) model and two-dimensional space (PDE) model. By examining a family of related models and trying to obtain similar predictions between these modelling frameworks, we establish that these phenomena are robust, and they are not restricted to specific details and assumptions of the models. Thus, comparing and contrasting the dynamics of different models can help in understanding the generality of ecological results [195], and may offer important insights into the robustness of model-based predictions of species' presence-absence.

Our work also highlights the importance of numerical continuation studies in tracking both stable and unstable steady states and bifurcation points in order to gain better understanding of the dynamics of ecological systems. We find that there are threshold values for ecologically-relevant parameters, which can lead to different outcomes of species interactions e.g. species coexistence, species exclusion and priority effects. For instance, in the case of intense biotic interactions, our finding suggests a theoretical explanation for the effect of dispersal on priority effects: while the steady-state characterised by the extinction of focal species is always stable, the steady-state corresponding to coexistence of species can lose its stability in a saddle-node bifurcation, as dispersal intensity changes. This bifurcation point indicates a threshold value in dispersal strength below which priority effects persist and lead to species coexistence.

Consistent with our observations, contrasting effects of dispersal has also been observed in ecological theory since the seminal work of Levin [126]: he examined the

dynamics of two species occupying coupled patches involving priority effects; he discovered a threshold mobility rate between these habitat patches. Above this threshold value, exclusion of species is possible; as dispersal decreases below this threshold value, this situation enhances the likelihood of species coexistence [126]. Similar observations have been demonstrated experimentally using microorganism communities. For instance, experimental studies [114] of competition and dispersal process between *E. coli.* species discussed in Chapter 1 discover that a weak dispersal can promote coexistence of the bacterial species [57]. It has also been observed in other experimental studies [35] that the survival of microorganism populations depend on dispersal strength: reducing dispersal promotes persistence of yeast population. Other studies [57], [160] with applications to bacterial communities have also highlighted a critical influence of dispersal on species diversity. In particular, Reichenbach et al. [160] establish the occurrence of a threshold dispersal strength: when dispersal exceeds this threshold value, species diversity is rapidly lost; however, when dispersal is lower than this threshold value, this situation promotes multi-species coexistence.

Closer examination of our results on different dispersal effects suggest that community composition is enhanced by local dispersal at moderate levels. In particular, we show that moderate dispersal enhances the zone of multi-species coexistence. This finding is in line with several results from the metacommunity framework [18], [191], which illustrate that an intermediate dispersal strength maximises species diversity. By using experimental metacommunities consisting of bacterial species, Venail et al. [191] show that dispersal in heterogeneous environments is important in the maintenance of biodiversity, with species diversity and productivity peak at medium dispersal levels. This moderate-level dispersal effect is also observed in our investigation using non-local dispersal models: intermediate-range dispersal can allow multi-species coexistence compared to short-range dispersal; however, species coexistence is lost when dispersal process occurs over larger spatial scales. These theoretical findings are consistent with some experimental observations: for instance, Cadotte [18] use metacommunities of microbial species connected by dispersal to explore the consequence of dispersal process occurring at different scales on species diversity; he shows that an intermediate dispersal distance enhances the richness of species, but in the cases of short-

or long-range dispersal, these situations can reduce species richness. By using experimental zooplankton metacommunities, Forbes and Chase [54] show that increasing dispersal can lead to a decrease in regional species diversity. Another important insight from this observation is the realisation that numerous factors can contribute to an understanding of species diversity, not only biotic interactions and abiotic variables, but the spatial scale of dispersal is also crucial.

From a species conservation perspective, a qualitative implication of our results is that connecting local habitats via movement corridors can have negative impacts for species diversity at several spatial scales. This observation is in line with research on metacommunities, which illustrates negative effects of dispersal on species diversity at larger spatial scale [19]. In practice, conservationists believe that increasing connectivity between habitat patches enhances the possibility of species survival [16], [123], [165]. Our results show that an increase in connectivity, however, can increase the risk of species extinction due to the rapid spread of superior species (e.g. competitors and invasive species) into local habitats; when dispersal occurs over larger spatial scales, this situation can also jeopardise species diversity due to the risk of landing in unsuitable habitats. Based on these observations, we suggest that the risk of dispersal-induced extinction should be should be taken into account in the design of such corridors as a conservation tool. This may require detailed knowledge of dispersal rates and biotic interactions, as well as information on dispersal patterns of species.

Our findings also demonstrate the influential roles of demographic stochasticity on community dynamics, and that in some situations, the stochastic model can exhibit different behaviour compared to its deterministic counterpart. We find that the occurrence of priority effects in stochastic models vary with population sizes: for small populations, there are fewer occurrences of priority effects in the stochastic models than in the deterministic models. Empirical studies [26] has illustrated that priority effects are less likely to appear in ecological systems with small populations, and these observations are in agreement with our theoretical findings. Furthermore, these results also illustrate an emergent behaviour of stochastic IBM, which can contribute to additional insights on the dynamics of species interactions. It also shows how such small-scale interactions coupled with local dispersal occurring at an individual-level

can affect population-level dynamics.

In sum, this study adds to our understanding of the strengths and weaknesses of different modelling approaches, and the possible implications on the predictions of species presence-absence. The mathematical models that we explored help us to better understand how the interplay of several ecological processes can combine to result in species coexistence and the occurrence of priority effects that strongly determine the presence-absence of species. It is hope that the insights from our theoretical models will open the door toward future works in range-limit research and further exploration of the influences of different ecological processes on multi-species community dynamics.

8.2 Future Work

Some open questions which have arisen during the course of this study are as follows. One obvious limitation of our studies is the assumptions of symmetric competitive strength and these species have the same dispersal rates. In reality, the interacting species can disperse at different rates depending on their dispersal ability. They can also exert different competitive pressure and empirical evidence suggests that the strength of competition is often asymmetric [33], [121]. It has been demonstrated in some studies [46], [58], [80] that differences in dispersal rates of competitive systems can modify the outcome of species interactions. Furthermore, previous studies have shown that asymmetric competitive strength [24], [177] may lead to different dynamical behaviours of the models, and thus can influence the observations of species presence-absence. For further research, it would be interesting to consider the unequal dispersal rates and asymmetric competition cases, and investigate the resulting dynamics of the systems.

In general, the models that we employ describe an example of biotic interactions, namely competition between multiple species along environmental gradients. In nature, apart from competition, there are numerous types of biotic interactions in multi-species ecosystems, such as prey-predator and mutualism, all of which can affect community assembly. Some studies [94] show that predation and competition can interact with dispersal to shape species range limits. It would be interesting to incorporate

these different kinds of biotic interactions into the models, and investigate how these biotic factors can combine with other to ecological forces (e.g. demographic stochasticity and dispersal process) to determine species presence-absence across heterogeneous environments.

Another intriguing aspect for future research is to validate our theoretical predictions on multi-species community dynamics in experimental studies. Some studies [69] have attempted to parametrise a two-species competition model extended along environmental gradients using experimental data from competing fruit fly species [37], [38]; they found that the range-limits of fruit flies predicted by their models are in agreement with the experimental studies [37], [38], particularly in the case of ecologically different competitors. Other studies [114] have explored the important roles of the spatial scale of ecological processes in maintaining species diversity; by employing experimental and theoretical approaches, they demonstrated that allowing ecological processes such as dispersal to occur over small (respectively, large) spatial scale can lead to coexistence (respectively, extinction) of species [114]. Based on this information, it would be interesting to investigate how the insights from our theoretical models would translate into species presence-absence emerging in real multi-species communities.

References

[1] M. Adamson and A. Y. Morozov, "Revising the role of species mobility in maintaining biodiversity in communities with cyclic competition", *Bulletin of mathematical biology*, vol. 74, no. 9, pp. 2004–2031, 2012.

[2] P. Adler, J. HilleRisLambers, and J. Levine, "A niche for neutrality", *Ecology letters*, vol. 10, no. 2, pp. 95–104, 2007.

[3] L. J. S. Allen and P. van den Driessche, "Relations between deterministic and stochastic thresholds for disease extinction in continuous- and discrete-time infectious disease models", *Mathematical Biosciences*, vol. 243, no. 1, pp. 99–108, 2013.

[4] L. J. S. Allen and G. E. Lahodny, "Extinction thresholds in deterministic and stochastic epidemic models", *Journal of Biological Dynamics*, vol. 6, no. 2, pp. 590–611, 2012.

[5] L. J. Allen, *An introduction to stochastic processes with applications to biology*. Pearson Education Upper Saddle River, NJ, 2003.

[6] L. J. Allen and E. J. Allen, "A comparison of three different stochastic population models with regard to persistence time", *Theoretical Population Biology*, vol. 64, no. 4, pp. 439–449, 2003.

[7] M. Alliende and J. Harper, "Demographic studies of a dioecious tree. i. colonization, sex and age structure of a population of salix cinerea", *The Journal of Ecology*, pp. 1029–1047, 1989.

[8] E. O. Alzahrani, F. A. Davidson, and N. Dodds, "A 3-species competition model for bio-control", *Applied Mathematics and Computation*, vol. 218, no. 19, pp. 9690–9698, 2012.

[9] P. Amarasekare and R. M. Nisbet, "Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species", *The American Naturalist*, vol. 158, no. 6, pp. 572–584, 2001.

[10] D. Andow, P. M. Kareiva, S. A. Levin, and A. Okubo, "Spread of invading organisms", *Landscape Ecology*, vol. 4, no. 2, pp. 177–188, 1990.

[11] V. Bahn, R. J O'Connor, and W. B Krohn, "Effect of dispersal at range edges on the structure of species ranges", *Oikos*, vol. 115, no. 1, pp. 89–96, 2006.

[12] J. P. Barry, C. H. Baxter, R. D. Sagarin, and S. E. Gilman, "Climate-related, long-term faunal changes in a california rocky intertidal community", *Science(Washington)*, vol. 267, no. 5198, pp. 672–675, 1995.

[13] A. Birand, A. Vose, and S. Gavrilets, "Patterns of species ranges, speciation, and extinction", *The American Naturalist*, vol. 179, no. 1, pp. 1–21, 2012.

[14] R. Bobbink, B. Beltman, J. Verhoeven, and D. Whigham, *Wetlands: Functioning, Biodiversity Conservation, and Restoration*. Springer Berlin Heidelberg, 2007.

[15] J. Brown and A. Kodric-Brown, "Turnover rates in insular biogeography: Effect of immigration on extinction.",

[16] L. A. Brudvig, E. I. Damschen, J. J. Tewksbury, N. M. Haddad, and D. J. Levey, "Landscape connectivity promotes plant biodiversity spillover into non-target habitats", *Proceedings of the National Academy of Sciences of the United States of America*, vol. 106, no. 23, pp. 9328–9332, 2009.

[17] T Burnett, "Effects of initial densities and periods of infestation on the growth-forms of a host and parasite population", *Canadian Journal of Zoology*, vol. 38, no. 6, pp. 1063–1077, 1960.

[18] M. W. Cadotte, "Metacommunity influences on community richness at multiple spatial scales: A microcosm experiment", *Ecology*, vol. 87, no. 4, pp. 1008–1016, 2006.

[19] M. W. Cadotte and T. Fukami, "Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape", *Ecology Letters*, vol. 8, no. 5, pp. 548–557, 2005.

[20] M. Cain, B. Milligan, and A. Strand, "Long-distance seed dispersal in plant populations", *American Journal of Botany*, vol. 87, no. 9, pp. 1217–1227, 2000.

[21] R. S. Cantrell and C. Cosner, "On the effects of spatial heterogeneity on the persistence of interacting species", *Journal of Mathematical Biology*, vol. 37, no. 2, pp. 103–145, 1998.

[22] R. Cantrell and C. Cosner, *Spatial Ecology via Reaction-Diffusion Equations*. Wiley, 2003.

[23] T. J. Case, R. D. Holt, M. A. McPeek, and T. H. Keitt, "The community context of species' borders: Ecological and evolutionary perspectives", *Oikos*, vol. 108, no. 1, pp. 28–46, 2005.

[24] T. Case, *An Illustrated Guide to Theoretical Ecology*. Oxford University Press, 2000.

[25] H. Caswell, R. Lensink, and M. G. Neubert, "Demography and dispersal: Life table response experiments for invasion speed", *Ecology*, vol. 84, no. 8, pp. 1968–1978, 2003.

[26] J. M. Chase, "Community assembly: When should history matter?", *Oecologia*, vol. 136, no. 4, pp. 489–498, 2003.

[27] P. Chesson, "Mechanisms of maintenance of species diversity", *Annual review of Ecology and Systematics*, vol. 31, pp. 343–358, 2000.

[28] J. Clobert, M. Baguette, T. Benton, J. Bullock, and S. Ducatez, *Dispersal ecology and evolution*. OUP Oxford, 2012.

[29] E. A. Codling, M. J. Plank, and S. Benhamou, "Random walk models in biology", *Journal of The Royal Society Interface*, vol. 5, no. 25, pp. 813–834, 2008.

[30] R. K. Colwell and D. C. Lees, "The mid-domain effect: Geometric constraints on the geography of species richness", *Trends in ecology & evolution*, vol. 15, no. 2, pp. 70–76, 2000.

[31] R. K. Colwell, C. Rahbek, and N. J. Gotelli, "The mid-domain effect and species richness patterns: What have we learned so far?", *The American Naturalist*, vol. 163, no. 3, E1–E23, 2004.

[32] L. Comte and G. Grenouillet, "Do stream fish track climate change? assessing distribution shifts in recent decades", *Ecography*, vol. 36, no. 11, pp. 1236–1246, 2013.

[33] J. H. Connell, "On the prevalence and relative importance of interspecific competition: Evidence from field experiments", *American Naturalist*, vol. 122, no. 5, pp. 661–696, 1983.

[34] J. H. Connell, "The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus", *Ecology*, vol. 42, no. 4, pp. 710–723, 1961.

[35] L. Dai, K. S. Korolev, and J. Gore, "Slower recovery in space before collapse of connected populations", *Nature*, vol. 496, no. 7445, pp. 355–358, 2013.

[36] C. Darwin, *On the origins of species by means of natural selection*. John Murray, 1859.

[37] A. J. Davis, L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood, "Making mistakes when predicting shifts in species range in response to global warming", *Nature*, vol. 391, no. 6669, pp. 783–786, 1998.

[38] A. J. Davis, J. H. Lawton, B. Shorrocks, and L. S. Jenkinson, "Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change", *Journal of Animal Ecology*, vol. 67, no. 4, pp. 600–612, 1998.

[39] G. Dayton and L. Fitzgerald, "Priority effects and desert anuran communities", *Canadian Journal of Zoology*, vol. 83, no. 8, pp. 1112–1116, 2005.

[40] N. De Meester, S. Derycke, A. Rigaux, and T. Moens, "Active dispersal is differentially affected by inter-and intraspecific competition in closely related nematode species", *Oikos*, vol. 124, no. 5, pp. 561–570, 2015.

[41] D. L. DeAngelis and Y Matsinos, "Individual-based population models: Linking behavioral and physiological information at the individual level to population dynamics", *Ecología Austral*, vol. 6, pp. 23–31, 1995.

[42] D. L. DeAngelis and W. M. Mooij, "Individual-based modeling of ecological and evolutionary processes", *Annual Review of Ecology, Evolution, and Systematics*, vol. 36, no. 1, pp. 147–168, 2005.

[43] A. J. Dennis, R. Green, and E. Schupp, *Seed dispersal: Theory and its application in a changing world*. CABI, 2007.

[44] U. Dieckmann, R. Law, and J. A. Metz, *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*. Cambridge University Press, 2000.

[45] T. Dobzhansky and S. Wright, "Genetics of natural populations. x. dispersion rates in drosophila pseudoobscura.", *Ecology*, vol. 28, no. 4, pp. 304–339, 2000.

[46] J. Dockery, V. Hutson, K. Mischaikow, and M. Pernarowski, "The evolution of slow dispersal rates: A reaction diffusion model", *Journal of Mathematical Biology*, vol. 37, no. 1, pp. 61–83, 1998.

[47] J. A. Drake, T. E. Flum, G. J. Witteman, T. Voskuil, A. M. Hoylman, C. Creson, D. A. Kenny, G. R. Huxel, C. S. Larue, and J. R. Duncan, "The construction and assembly of an ecological landscape", *Journal of Animal Ecology*, pp. 117–130, 1993.

[48] C. Dytham, "Evolved dispersal strategies at range margins", *Proceedings of the Royal Society of London B: Biological Sciences*, vol. 276, no. 1661, pp. 1407–1413, 2009.

[49] R. Etienne, B. Wertheim, L. Hemerik, P Schneider, and J. Powell, "The interaction between dispersal, the allee effect and scramble competition affects population dynamics.", *Ecological Modelling*, vol. 148, no. 2, pp. 153–168, 2002.

[50] B. Faugeras and O. Maury, "Modeling fish population movements: From an individual-based representation to an advection-diffusion equation", *Journal of Theoretical Biology*, vol. 247, no. 4, pp. 837–848, 2007.

[51] G. P. Figueredo, P.-O. Siebers, and U. Aickelin, "Investigating mathematical models of immuno-interactions with early-stage cancer under an agent-based modelling perspective", *BMC bioinformatics*, vol. 14, no. Suppl 6, S6, 2013.

[52] G. P. Figueredo, P.-O. Siebers, M. R. Owen, J. Reps, and U. Aickelin, "Comparing stochastic differential equations and agent-based modelling and simulation for early-stage cancer", *PloS one*, vol. 9, no. 4, e95150, 2014.

[53] R. A. Fisher, "The wave of advance of advantageous genes", *Annals of Eugenics*, vol. 7, no. 4, pp. 355–369, 1937.

[54] A. E. Forbes and J. M. Chase, "The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities", *Oikos*, vol. 96, no. 3, pp. 433–440, 2002.

[55] C. Fraser, S. Banks, and J. Waters, "Priority effects can lead to underestimation of dispersal and invasion potential", *Biological Invasions*, vol. 17, no. 1, pp. 1–8, 2015.

[56] D. Fraser, J. Gilliam, M. Daley, A. Le, and G. Skalski, "Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration.", *The American Naturalist*, vol. 158, no. 2, pp. 124–135, 2001.

[57] E. Frey, "Evolutionary game theory: Theoretical concepts and applications to microbial communities", *Physica A: Statistical Mechanics and its Applications*, vol. 389, no. 20, pp. 4265–4298, 2010.

[58] A. Friedman and C. Cosner, *Tutorials in Mathematical Biosciences IV Evolution and Ecology*. Springer Science and Business Media, 2007.

[59] C. Fritsch, J. Harmand, and F. Campillo, "A modeling approach of the chemostat", *Ecological Modelling*, vol. 299, pp. 1–13, 2015.

[60] K. J. Gaston, "Geographic range limits of species", *Proceedings of the Royal Society of London B: Biological Sciences*, vol. 276, no. 1661, pp. 1391–1393, 2009.

[61] K. J. Gaston, *The structure and dynamics of geographic ranges*. Oxford University Press, 2003.

[62] K. Gaston and F. He, "The distribution of species range size: A stochastic process", *Proceedings of the Royal Society. B, Biological sciences*, vol. 269, no. 1495, pp. 1079–1086, 2002.

[63] G. F. Gause, "Experimental studies on the struggle for existence", *Journal of experimental biology*, vol. 9, no. 4, pp. 389–402, 1932.

[64] G. Gause, *The struggle for existence*. Dover Publications, 1934.

[65] I. Geijzendorffer, W Van der Werf, F. Bianchi, and R. Schulte, "Sustained dynamic transience in a Lotka-Volterra competition model system for grassland species", *Ecological Modelling*, vol. 222, no. 15, pp. 2817–2824, 2011.

[66] D. Gerla, M. Vos, B. Kooi, and W. Mooij, "Effects of resources and predation on the predictability of community composition", *Oikos*, vol. 118, no. 7, pp. 1044–1052, 2009.

[67] S. E. Gilman, M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt, "A framework for community interactions under climate change", *Trends in Ecology and Evolution*, vol. 25, no. 6, pp. 325–331, 2010.

[68] P. Gómez-Mourelo, "From individual-based models to partial differential equations: An application to the upstream movement of elvers", *Ecological modelling*, vol. 188, no. 1, pp. 93–111, 2005.

[69] W. Godsoe, R. Murray, and M. Plank, "Information on biotic interactions improves transferability of distribution models", *The American Naturalist*, vol. 185, no. 2, pp. 281–290, 2015.

[70] W. Godsoe, R. Murray, and M. J. Plank, "The effect of competition on species' distributions depends on coexistence, rather than scale alone", *Ecography*, vol. 38, no. 11, pp. 1071–1079, 2015.

[71] A Gonzalez, J. Lawton, F. Gilbert, T. Blackburn, and I Evans-Freke, "Metapopulation dynamics, abundance, and distribution in a microecosystem", *Science*, vol. 281, no. 5385, pp. 2045–2047, 1998.

[72] N. J. Gotelli, *A primer of ecology*. Sinauer Associates Incorporated, 1995.

[73] P. Gregory, "Interpreting plant disease dispersal gradients", *Annual Review of Phytopathology*, vol. 6, no. 1, pp. 189–212, 1968.

[74] V. Grimm, "Ten years of individual-based modelling in ecology: What have we learned and what could we learn in the future?", *Ecological Modelling*, vol. 115, no. 2, pp. 129–148, 1999.

[75] J. Grinnell, "The niche-relationships of the california thrasher", *The Auk*, vol. 34, no. 4, pp. 427–433, 1917.

[76] E. D. Grosholz, "Contrasting rates of spread for introduced species in terrestrial and marine systems", *Ecology*, vol. 77, no. 6, pp. 1680–1686, 1996.

[77] N. B. Grow, S. Gursky-Doyen, and A. Krzton, *High altitude primates*. Springer, 2014.

[78] A. Guisan and W. Thuiller, "Predicting species distribution: Offering more than simple habitat models", *Ecology Letters*, vol. 8, no. 9, pp. 993–1009, 2005.

[79] A. Guisan, R. Tingley, J. B. Baumgartner, I. Naujokaitis-Lewis, P. R. Sutcliffe, A. I. Tulloch, T. J. Regan, L. Brotons, E. McDonald-Madden, and C. Mantyka-Pringle, "Predicting species distributions for conservation decisions", *Ecology Letters*, vol. 16, no. 12, pp. 1424–1435, 2013.

[80] R. Hambrock and Y. Lou, "The evolution of conditional dispersal strategies in spatially heterogeneous habitats", *Bulletin of Mathematical Biology*, vol. 71, no. 8, pp. 1793–1817, 2009.

[81] A. Hampe and A. S. Jump, "Climate relicts: Past, present, future", *Annual Review of Ecology, Evolution, and Systematics*, vol. 42, no. 1, pp. 313–333, 2011.

[82] I. Hanski, "Metapopulation dynamics", *Nature*, vol. 396, no. 6706, pp. 41–49, 1998.

[83] C. D. Harley, "Climate change, keystone predation, and biodiversity loss", *Science*, vol. 334, no. 6059, pp. 1124–1127, 2011.

[84] A. Hastings and L. J. Gross, *Encyclopedia of theoretical ecology*. Univ of California Press, 2012.

[85] G. Hetzer, T. Nguyen, and W. Shen, "Coexistence and extinction in the volterra-lotka competition model with nonlocal dispersal.", *Communications on Pure & Applied Analysis*, vol. 11, no. 5, 2012.

[86] R. Hickson, S. Barry, and K. Stokes, "Comparison of weed spread models.", *ANZIAM Journal*, vol. 49, pp. 324–340, 2008.

[87] D. Hiebeler, "Competition between near and far dispersers in spatially structured habitats", *Theoretical Population Biology*, vol. 66, no. 3, pp. 205–218, 2004.

[88] S. I. Higgins and D. M. Richardson, "Predicting plant migration rates in a changing world: The role of long-distance dispersal", *The American Naturalist*, vol. 153, no. 5, pp. 464–475, 1999.

[89] T. Hillen, B. Greese, J. Martin, and G. de Vries, "Birth-jump processes and application to forest fire spotting", *Journal of biological dynamics*, vol. 9, no. sup1, pp. 104–127, 2015.

[90] J. HilleRisLambers, M. A. Harsch, A. K. Ettinger, K. R. Ford, and E. J. Theobald, "How will biotic interactions influence climate change-induced range shifts?", *Annals of the New York Academy of Sciences*, vol. 1297, no. 1, pp. 112–125, 2013.

[91] J. Hiscox, M. Savoury, C. Müller, B. Lindahl, H. Rogers, and L. Boddy, "Priority effects during fungal community establishment in beech wood", *The ISME journal.*, vol. 9, no. 10, pp. 1–15, 2015.

[92] E. Holmes and H. Wilson, "Running from trouble: Long-distance dispersal and the competitive coexistence of inferior species", *The American Naturalist*, vol. 151, no. 6, pp. 578–586, 1998.

[93] E. E. Holmes, M. A. Lewis, J. Banks, and R. Veit, "Partial differential equations in ecology: Spatial interactions and population dynamics", *Ecology*, vol. 75, no. 1, pp. 17–29, 1994.

[94] R. D. Holt and M. Barfield, "Trophic interactions and range limits: The diverse roles of predation", *Proceedings of the Royal Society B-Biological Sciences*, vol. 276, no. 1661, pp. 1435–1442, 2009.

[95] R. D. Holt, T. H. Keitt, M. A. Lewis, B. A. Maurer, and M. L. Taper, "Theoretical models of species-borders: Single species approaches", *Oikos*, vol. 108, no. 1, pp. 18–27, 2005.

[96] T. Horton, D. Swaney, and T. Galante, "Dispersal of ectomycorrhizal basidiospores: The long and short of it.", *Mycologia*, vol. 105, no. 6, pp. 1623–1626, 2013.

[97] P Howard, "Analysis of ode models", 2009.

[98] H. F. Howe and J. Smallwood, "Ecology of seed dispersal", *Annual review of ecology and systematics*, vol. 13, pp. 201–228, 1982.

[99] S. Hubbell, *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, 2001.

[100] G. E. Hutchinson, "Concluding remarks", in *Cold Spring Harbor Symposium on Quantitative Biology*, vol. 22, Cold Spring Harbor Laboratory Press, 1957, pp. 415–427.

[101] V. Hutson, S. Martinez, K. Mischaikow, and G. Vickers, "The evolution of dispersal", *Journal of mathematical biology*, vol. 47, no. 6, pp. 483–517, 2003.

[102] S. Jeffries, H. Huber, J. Calambokidis, and J. Laake, "Trends and status of harbor seals in washington state: 1978-1999", *The Journal of Wildlife Management*, pp. 207–218, 2003.

[103] D. Johnson, "Priorities for research on priority effects", *New Phytologist*, vol. 205, no. 4, pp. 1375–1377, 2015.

[104] J. L. Johnson and J. E. Havel, "Competition between native and exotic daphnia: In situ experiments", *Journal of Plankton Research*, vol. 23, no. 4, pp. 373–387, 2001.

[105] W. A. Jones, S. Greenberg, and B Legaspi Jr, "The effect of varying bemisia argentifolii and eretmocerus mundus ratios on parasitism", *BioControl*, vol. 44, no. 1, pp. 13–28, 1999.

[106] S. E. Jorgensen and B. Fath, *Encyclopedia of ecology*. Newnes, 2014.

[107] A. Kandler and R. Unger, *Population Dispersal Via Diffusion-reaction Equations*. Techn. Univ., Fak. für Mathematik, 2010.

[108] C.-Y. Kao, Y. Lou, and W. Shen, "Random dispersal vs. nonlocal dispersal", *Discrete and Continuous Dynamical Systems*, vol. 26, no. 2, pp. 551–596, 2010.

[109] C. Kao, Y. Lou, and W. Shen, "Evolution of mixed dispersal in periodic environments.", *Discrete Contin. Dyn. Syst. Ser. B*, vol. 17, no. 6, pp. 2047–2072, 2012.

[110] P. Kardol, L. Souza, and A. Classen, "Resource availability mediates the importance of priority effects in plant community assembly and ecosystem function", *Oikos*, vol. 122, no. 1, pp. 84–94, 2013.

[111] P. Kareiva, "Experimental and mathematical analyses of herbivore movement: Quantifying the influence of plant spacing and quality on foraging discrimination", *Ecological Monographs*, vol. 52, no. 3, pp. 261–282, 1982.

[112] M. Kearney and W. Porter, "Mechanistic niche modelling: Combining physiological and spatial data to predict species-ranges", *Ecology Letters*, vol. 12, no. 4, pp. 334–350, 2009.

[113] P. Kennedy, K. Peay, and T. Bruns, "Root tip competition among ectomycorrhizal fungi: Are priority effects a rule or an exception?", *Ecology*, vol. 90, no. 8, pp. 2098–2107, 2009.

[114] B. Kerr, M. Riley, M. Feldman, and B. Bohannan, "Local dispersal promotes biodiversity in a real-life game of rock–paper–scissors", *Nature*, vol. 418, no. 6894, pp. 171–174, 2002.

[115] M. Kessler, "Patterns of diversity and range size of selected plant groups along an elevational transect in the bolivian andes", *Biodiversity & Conservation*, vol. 10, no. 11, pp. 1897–1921, 2001.

[116] B. Kooi, M. Boer, and S. Kooijman, "Resistance of a food chain to invasion by a top predator", *Mathematical Biosciences*, vol. 157, no. 1, pp. 217–236, 1999.

[117] M. Kot, M. Lewis, and P. van den Driessche, "Dispersal data and the spread of invading organisms", *Ecology*, vol. 77, no. 7, pp. 2027–2042, 2000.

[118] M. Kot, *Elements of mathematical ecology*. Cambridge University Press, 2001.

[119] A. M. Kramer, M. M. Lyons, F. C. Dobbs, and J. M. Drake, "Bacterial colonization and extinction on marine aggregates: Stochastic model of species presence and abundance", *Ecology and evolution*, vol. 3, no. 13, pp. 4300–4309, 2013.

[120] R. Law, D. J. Murrell, and U. Dieckmann, "Population growth in space and time: Spatial logistic equations", *Ecology*, vol. 84, no. 1, pp. 252–262, 2003.

[121] J. Lawton and M. Hassell, "Asymmetrical competition in insects", *Natute*, vol. 289, no. 5800, pp. 793–795, 1981.

[122] G. Lei and I. Hanski, "Spatial dynamics of two competing specialist parasitoids in a host metapopulation", *Journal of Animal Ecology*, vol. 67, no. 3, pp. 422–433, 1998.

[123] D. J. Levey, B. M. Bolker, J. J. Tewksbury, S. Sargent, and N. M. Haddad, "Effects of landscape corridors on seed dispersal by birds", *Science*, vol. 309, no. 5731, pp. 146–148, 2005.

[124] S. Levin, S. Carpenter, H. Godfray, A. Kinzig, M. Loreau, J. Losos, B. Walker, and D. Wilcove, *The Princeton Guide to Ecology*. Princeton University Press, 2009.

[125] S. Levin, H. Muller-Landau, R. Nathan, and J. Chave, "The ecology and evolution of seed dispersal: A theoretical perspective", *Annual Review of Ecology, Evolution, and Systematics*, vol. 34, pp. 575–604, 2003.

[126] S. A. Levin, "Dispersion and population interactions", *The American Naturalist*, vol. 108, no. 960, pp. 207–228, 1974.

[127] M. A. Lewis, S. V. Petrovskii, and J. R. Potts, *The Mathematics Behind Biological Invasions*. Springer, 2016, vol. 44.

[128] G. Livingston, M. Matias, V. Calcagno, C. Barbera, M. Combe, M. A. Leibold, and N. Mouquet, "Competition-colonization dynamics in experimental bacterial metacommunities", *Nature Communications*, vol. 3, p. 1234, 2012.

[129] A. J. Lotka, *Elements of physical biology*. Williams and Wilkins, 1925.

[130] C. Loureiro, J. Pereira, M. Pedrosa, F. Goncalves, and B. Castro, "Competitive outcome of daphnia-simocephalus experimental microcosms: Salinity versus priority effects", *PloS one*, vol. 8, no. 8, pp. 1–7, 2013.

[131] F. Lutscher, "Nonlocal dispersal and averaging in heterogeneous landscapes", *Applicable Analysis*, vol. 89, no. 7, pp. 1091–1108, 2010.

[132] N. Mabrouk, "Analyzing individual-based models of microbial systems", PhD thesis, Université Blaise Pascal, 2010.

[133] W. P. MacLean and R. D. Holt, "Distributional patterns in st. croix sphaerodactylus lizards: The taxon cycle in action", *Biotropica*, vol. 11, no. 3, pp. 189–195, 1979.

[134] C. P. Madenjian, D. W. Schloesser, and K. A. Krieger, "Population models of burrowing mayfly recolonization in western lake erie", *Ecological Applications*, vol. 8, no. 4, pp. 1206–1212, 1998.

[135] H. Matano, "Asymptotic behavior and stability of solutions of semilinear diffusion equations.", *Publications of the Research Institute for Mathematical Sciences,*, vol. 15, no. 2, pp. 401–454, 1979.

[136] B. Matthiessen, E. Mielke, and U. Sommer, "Dispersal decreases diversity in heterogeneous metacommunities by enhancing regional competition", *Ecology*, vol. 91, no. 7, pp. 2022–2033, 2010.

[137] C. M. McCain, "Elevational gradients in diversity of small mammals", *Ecology*, vol. 86, no. 2, pp. 366–372, 2005.

[138] ——, "The mid-domain effect applied to elevational gradients: Species richness of small mammals in costa rica", *Journal of Biogeography*, vol. 31, no. 1, pp. 19–31, 2004.

[139] M Mimura, S.-I. Ei, and Q Fang, "Effect of domain-shape on coexistence problems in a competition-diffusion system", *Journal of Mathematical Biology*, vol. 29, no. 3, pp. 219–237, 1991.

[140] G. Mittelbach, *Community Ecology*. Sinauer Associates, Incorporated, 2012.

[141] M. H. Mohd, R. Murray, M. J. Plank, and W. Godsoe, "Effects of dispersal and stochasticity on the presence–absence of multiple species", *Ecological Modelling*, vol. 342, pp. 49–59, 2016.

[142] P. J. Morin, *Community ecology*. John Wiley & Sons, 2011.

[143] C. Moritz, J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger, "Impact of a century of climate change on small-mammal communities in yosemite national park, USA", *Science*, vol. 322, no. 5899, pp. 261–264, 2008.

[144] A. Morozov and B. Li, "On the importance of dimensionality of space in models of space-mediated population persistence.", *Theoretical population biology*, vol. 71, no. 3, pp. 278–289, 2007.

[145] J. Murray, *Mathematical Biology I: An Introduction*. Springer-Verlag, 2002.

[146] T. Namba, "Dispersal-mediated coexistence of indirect competitors in source-sink metacommunities", *Japan journal of industrial and applied mathematics*, vol. 24, no. 1, pp. 39–55, 2007.

[147] R. Nathan and H. Muller-Landau, "Spatial patterns of seed dispersal, their determinants and consequences for recruitment", *Trends in ecology evolution*, vol. 15, no. 7, pp. 278–285, 2000.

[148] M. Neubert and H. Caswell, "Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations.", *Ecology*, vol. 81, no. 6, pp. 1613–1628, 2000.

[149] R. Nisbet and W. Gurney, *Modelling fluctuating populations*. Wiley, 1982.

[150] A. Okubo, P. K. Maini, M. H. Williamson, and J. D. Murray, "On the spatial spread of the grey squirrel in Britain", *Proceedings of the Royal Society of London. Series B, Biological Sciences*, vol. 238, no. 1291, pp. 113–125, 1989.

[151] S. P. Otto and T. Day, *A biologist's guide to mathematical modeling in ecology and evolution*. Princeton University Press, 2007, vol. 13.

[152] S. W. Pacala, "Neighborhood models of plant population dynamics. 2. multi-species models of annuals", *Theoretical Population Biology*, vol. 29, no. 2, pp. 262–292, 1986.

[153] E. Paradis, S. Baillie, W. Sutherland, and R. Gregory, "Patterns of natal and breeding dispersal in birds.", *Journal of Animal Ecology*, vol. 67, no. 4, pp. 518–536, 1998.

[154] T. Park, "Experimental studies of interspecies competition ii. temperature,humidity, and competition in two species of tribolium", *Physiological Zoology*, vol. 27, no. 3, pp. 177–238, 1954.

[155] T. Park, D. Mertz, W. Grodzinski, and T. Prus, "Cannibalistic predation in populations of flour beetles", *Physiological Zoology*, vol. 38, no. 3, pp. 289–321, 1965.

[156] I. G. Pearce, M. A. J. Chaplain, P. G. Schofield, A. R. A. Anderson, and S. F. Hubbard, "Modelling the spatio-temporal dynamics of multi-species host-parasitoid interactions: Heterogeneous patterns and ecological implications", *Journal of Theoretical Biology*, vol. 241, no. 4, pp. 876–886, 2006.

[157] R. G. Pearson and T. P. Dawson, "Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful?", *Global ecology and biogeography*, vol. 12, no. 5, pp. 361–371, 2003.

[158] A. L. Perry, P. J. Low, J. R. Ellis, and J. D. Reynolds, "Climate change and distribution shifts in marine fishes", *Science*, vol. 308, no. 5730, pp. 1912–1915, 2005.

[159] H. R. Pulliam, "On the relationship between niche and distribution", *Ecology Letters*, vol. 3, no. 4, pp. 349–361, 2000.

[160] T. Reichenbach, M. Mobilia, and E. Frey, "Mobility promotes and jeopardizes biodiversity in rock–paper–scissors games", *Nature*, vol. 448, no. 7157, pp. 1046–1049, 2007.

[161] E. Renshaw, *Modelling Biological Populations in Space and Time*. Cambridge University Press, 1993.

[162] T. Root, *Atlas of wintering North American birds*. University of Chicago Press, 1988.

[163] ——, "Environmental factors associated with avian distributional boundaries", *Journal of Biogeography*, vol. 15, no. 3, pp. 489–505, 1988.

[164] J. Roughgarden, *Theory of population genetics and evolutionary ecology: An introduction*. Macmillan Publishing, 1979.

[165] K. Salau, M. L. Schoon, J. A. Baggio, and M. A. Janssen, "Varying effects of connectivity and dispersal on interacting species dynamics", *Ecological Modelling*, vol. 242, pp. 81–91, 2012.

[166] K. V. I. Saputra, L. Van Veen, and G. R. W. Quispel, "The saddle-node-transcritical bifurcation in a population model with constant rate harvesting", *Dynamics of Continuous Discrete and Impulsive Systems-Series B-Mathematical Analysis*, vol. 14, pp. 233–250, 2010.

[167] J. P. Sexton, P. J. McIntyre, A. L. Angert, and K. J. Rice, "Evolution and ecology of species range limits", *Annual Review of Ecology Evolution and Systematics*, vol. 40, no. 1, pp. 415–436, 2009.

[168] N. Shigesada and K. Kawasaki, *Biological invasions: Theory and practice*. Oxford University Press, 1997.

[169] A. Shmida and M. V. Wilson, "Biological determinants of species diversity", *Journal of Biogeography*, pp. 1–20, 1985.

[170] J. B. Shurin, P. Amarasekare, J. M. Chase, R. D. Holt, M. F. Hoopes, and M. A. Leibold, "Alternative stable states and regional community structure", *Journal of Theoretical Biology*, vol. 227, no. 3, pp. 359–368, 2004.

[171] J. L. Simonis, "Demographic stochasticity reduces the synchronizing effect of dispersal in predator-prey metapopulations", *Ecology*, vol. 93, no. 7, pp. 1517–1524, 2012.

[172] J. Skellam, "Random dispersal in theoretical populations", *Biometrika*, pp. 196–218, 1951.

[173] J. Soberón, "Grinnellian and eltonian niches and geographic distributions of species", *Ecology Letters*, vol. 10, no. 12, pp. 1115–1123, 2007.

[174] F. A. L. Sorte and F. R. Thompson III, "Poleward shifts in winter ranges of North American birds", *Ecology*, vol. 88, no. 7, pp. 1803–1812, 2007.

[175] T. L. Staples, J. M. Dwyer, X. Loy, and M. M. Mayfield, "Potential mechanisms of coexistence in closely related forbs", *Oikos*, 2016.

[176] A. Steyn-Ross and M. Steyn-Ross, *Modeling phase transitions in the brain*. Springer, 2010.

[177] C. Strobeck, "N species competition", *Ecology*, vol. 54, no. 3, pp. 650–654, 1973.

[178] S. H. Strogatz, "Nonlinear dynamics and chaos: With applications to physics, biology, chemistry, and engineering (studies in nonlinearity)", 2001.

[179] K. Suttle, M. A. Thomsen, and M. E. Power, "Species interactions reverse grassland responses to changing climate", *Science*, vol. 315, no. 5812, pp. 640–642, 2007.

[180] J.-C. Svenning, D. Gravel, R. D. Holt, F. M. Schurr, W. Thuiller, T. Münkemüller, K. H. Schiffers, S. Dullinger, T. C. Edwards, T. Hickler, S. I. Higgins, J. E. M. S. Nabel, J. Pagel, and S. Normand, "The influence of interspecific interactions on species range expansion rates", *Ecography*, vol. 12, no. 37, pp. 1198–1209, 2014.

[181] C. Symons and S. Arnott, "Timing is everything: Priority effects alter community invasibility after disturbance.", *Ecology and evolution*, vol. 4, no. 4, pp. 397–407, 2014.

[182] T.-w. Tam and P. O. Ang, "Object-oriented simulation of coral competition in a coral reef community", *Ecological Modelling*, vol. 245, no. 0, pp. 111–120, 2012.

[183] S. Tang, G. Tang, and R. A. Cheke, "Optimum timing for integrated pest management: Modelling rates of pesticide application and natural enemy releases", *Journal of Theoretical Biology*, vol. 264, no. 2, pp. 623–638, 2010.

[184] H. M. Taylor and S. Karlin, *An introduction to stochastic modeling*. Elsevier Science, 2014.

[185] D. Tilman, "Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly", *Proceedings of the National Academy of Sciences of the United States of America*, vol. 101, no. 30, pp. 10 854–10 861, 2004.

[186] M. C. Urban, J. J. Tewksbury, and K. S. Sheldon, "On a collision course: Competition and dispersal differences create no-analogue communities and cause extinctions during climate change", *Proceedings of the Royal Society B: Biological Sciences*, vol. 279, no. 1735, pp. 2072–2080, 2012.

[187] S. Van Bael and S. Pruett-Jones, "Exponential population growth of monk parakeets in the united states", *The Wilson Bulletin*, pp. 584–588, 1996.

[188] E. H. Van Nes and M. Scheffer, "Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift", *The American Naturalist*, vol. 169, no. 6, pp. 738–747, 2007.

[189] G. Van Voorn and B. Kooi, "Smoking epidemic eradication in a eco-epidemiological dynamical model", *Ecological Complexity*, vol. 14, pp. 180–189, 2013.

[190] J. H. Vandermeer, "The competitive structure of communities: An experimental approach with protozoa", *Ecology*, vol. 50, no. 3, pp. 362–371, 1969.

[191] P. Venail, R. MacLean, T Bouvier, M. Brockhurst, M. Hochberg, and N Mouquet, "Diversity and productivity peak at intermediate dispersal rate in evolving metacommunities", *Nature*, vol. 452, no. 7184, pp. 210–214, 2008.

[192] P. F. Verhulst, "Recherches mathématiques sur la loi d'accroissement de la population.", *Nouveaux Mémoires de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles*, vol. 18, pp. 14–54, 1845.

[193] V. Volterra, "Fluctuations in the abundance of a species considered mathematically", *Nature*, vol. 118, pp. 558–560, 1926.

[194] G. d. Vries, *A Course in Mathematical Biology: Quantitative Modeling with Mathematical and Computational Methods*. Society for Industrial and Applied Mathematics, 2006.

[195] M. Weisberg and K. Reisman, "The robust Volterra principle", *Philosophy of Science*, vol. 75, no. 1, pp. 106–131, 2008.

[196] J. J. Wiens, "The niche, biogeography and species interactions", *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 366, no. 1576, pp. 2336–2350, 2011.

[197] W. Wilson, E McCauley, and A. De Roos, "Effect of dimensionality on Lotka-Volterra predator-prey dynamics: Individual based simulation results", *Bulletin of Mathematical Biology*, vol. 57, no. 4, pp. 507–526, 1995.

[198] W. G. Wilson, "Resolving discrepancies between deterministic population models and individual-based simulations", *The American Naturalist*, vol. 151, no. 2, pp. 116–134, 1998.

[199] M. S. Wisz, J. Pottier, W. D. Kissling, L. Pellissier, J. Lenoir, C. F. Damgaard, C. F. Dormann, M. C. Forchhammer, J.-A. Grytnes, and A. Guisan, "The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling", *Biological Reviews*, vol. 88, no. 1, pp. 15–30, 2013.

[200] M. J. Wittmann, W. Gabriel, E.-M. Harz, C. Laforsch, and J. M. Jeschke, "Can daphnia lumholtzi invade European lakes?", *NeoBiota*, no. 16, pp. 39–57, 2013.

[201] X. Ye, A. K. Skidmore, and T. Wang, "Joint effects of habitat heterogeneity and species' life-history traits on population dynamics in spatially structured landscapes", *PloS one*, vol. 9, no. 9, e107742, 2014.

[202] P. L. Zarnetske, T. C. Gouhier, S. D. Hacker, E. W. Seabloom, and V. A. Bokil, "Indirect effects and facilitation among native and non-native species promote invasion success along an environmental stress gradient", *Journal of Ecology*, vol. 101, no. 4, pp. 905–915, 2013.